DETERMINING BIOLOGICAL SOURCES OF VARIATION IN RESIDUAL FEED INTAKE IN BRAHMAN HEIFERS DURING CONFINEMENT FEEDING AND ON PASTURE

A Thesis

by

ROBERT O. DITTMAR III

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

December 2007

Major Subject: Physiology of Reproduction

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ABSTRACT

Determining Biological Sources of Variation in Residual Feed Intake in Brahman Heifers During Confinement Feeding and on Pasture. (December 2007)

Robert O. Dittmar III, B.S., Texas A&M University

Co-Chairs of Advisory Committee: Dr. R. D. Randel
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Objectives were to characterize residual feed intake (RFI) and determine the phenotypic correlation between performance, feed efficiency, and other biological measurements in Brahman heifers, as well as the relationship between RFI determined in confinement and measurements of grazing activity on pasture. Three separate 70 d feeding trials were performed, and RFI was determined as the residual between actual and predicted dry matter intake (DMI) for a given level of production. Brahman heifers (n = 103; 5-to-9 mo of age) were individually limit-fed a pelleted 12% CP complete ration daily in Calan gates. Weekly body weight (BW) and DMI data were collected, and predicted DMI was determined by linear regression of actual DMI on mid-test metabolic BW. Ytterbium chloride was used to evaluate digestive kinetics, and fecal samples were collected to determine fecal volatile fatty acids (VFA) concentration and determine apparent dry matter digestibility (DMD) utilizing acid insoluble ash as an internal marker. Measurements of temperament were evaluated on all heifers at weaning. High (n = 6) and low (n = 6) RFI heifers (Exp. I) grazed fescue and ryegrass to determine variation in grazing behavior, DMI, and apparent DMD.

Data from all three experiments were pooled, and RFI was not correlated with average daily gain (ADG), DMI, BW, partial efficiency of gain, feed conversion ration, fecal VFA concentration, or any measures of temperament. There were no significant differences in digestive kinetics between the RFI efficiency groups. Fecal samples taken for acid detergent insoluble ash (ADIA) determination were not collected at frequent enough intervals to account for weekly variation in fecal ADIA concentration. Pasture measurements were not different between the efficiency groups for heifers evaluated for grazing behavior, as well as estimated intake as a proportion of BW, or apparent DMD. Results of this study suggest that *Bos indicus* cattle appear to have similar efficiency traits as *Bos taurus* and *Bos indicus* influenced cattle, making this measure of efficiency equally as valid for use in both types of cattle. This indicates that selection based on RFI can be made to increase feed efficiency without affecting ADG or BW in Brahman cattle.

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CHAPTER I

INTRODUCTION AND LITERATURE REVIEW

Introduction

The fiscal goal of most beef producers is to maximize profitability by optimizing output or gain, while decreasing inputs. The profit margin for a beef producer is the difference between the income they receive for sale of animals, and the cost of inputs required in producing those animals. Providing feed to livestock is a major contributor to the cost associated with the inputs of production, making it an area that can have a significant affect on profitability. Efficient utilization of feed provided to animals by the producer will cost-effectively increase production. In order to accomplish this, producers must select for more efficient animals. There are many feed efficiency traits that have been used to describe efficient and inefficient animals. However, some of these measurements are calculated with, and are directly related to growth rate. Selection based on these types of measures potentially could lead to increases in rate of gain and mature weight. An increase in mature weight may become a problem if the producer is unable to support the maintenance requirements associated with the increase in size. Physiological and behavioral differences have been noted between efficient and inefficient animals. Understanding causes for those differences between animals of varying efficiency will help select and better manage efficient beef cattle. Identification of potential variation between efficiency groups may be used as an indicator to better

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This thesis follows the style of Journal of Animal Science.

identify an animal's level of efficiency in a production setting, without the need for lengthy feeding trials. Understanding the relationship between grazing behavior and forage intake on pasture and residual feed intake (RFI) determined in confinement will improve our understanding of how efficient animals perform in a production setting. Determining and defining all of the sources of variation associated with differences in feed efficiency, and how different measures of feed efficiency relate to one another, will allow producers to make better decisions on how to market and manage their animals.

Measures of Feed Efficiency

Feed Conversion Ratio. Feed conversion ratio (FCR), developed by Brody (1945) as cited by Nkrumah et al. (2004), is perhaps the most common measure of feed efficiency utilized in beef cattle production (Archer et al., 1999; Nkrumah et al., 2004). Efficiency based on FCR is calculated as the ratio of feed consumption to live-weight gain (Table 1.1; Arthur et al., 1996; Arthur et al., 2001a). A low FCR ratio indicates increased feed efficiency, because it takes less feed input to produce a unit of gain than an animal with a high FCR, requiring more feed input to produce that same unit of gain. This measure has some potential drawbacks that could have a negative impact on production. Numerous studies have shown (Koots et al., 1994; Arthur et al., 2001a, b; Hennessy and Arthur, 2004; Nkrumah et al., 2004) that FCR is negatively correlated to average daily gain (ADG; Table 1.2). This means that selection for FCR may result in an increase in animal body weight (BW), which for some producers is not always a desirable trait. Arthur et al. (1996) states that any attempt to accurately measure feed efficiency must take into account requirements for both maintenance and gain. Feed

Table 1.1. Definition of feed efficiency traits[a]

Feed Efficiency Trait	Definition	Calculation	Desired Phenotype
Feed conversion ratio (FCR)	Feed intake required to produce one unit of weight gain.	DMI ÷ ADG	Low
Partial efficiency of growth (PEG)	Efficiency of BW gain after maintenance requirements have been accounted for.	ADG ÷ (Actual DMI – DMI required for maintenance) when maintenance is calculated as $0.077 \times BW^{0.75} \div NE_m$ concentration of the diet (NRC, 2000)	High
Residual feed intake (RFI)	Difference in expected DMI for maintenance and growth at a given level of production and actual DMI	DMI – Expected DMI, where expected DMI is obtained by the regression of DMI on mid-test metabolic BW and ADG	Low

[a]Adapted from Arthur et al. (2001b), Hennessy and Arthur (2004), and Brown (2005).

Table 1.2. Phenotypic correlations between measures of feed efficiency and measures of performance in beef cattle[a]

FCR			PEG			RFI					
ADG	BW	DMI	ADG	BW	DMI	ADG	BW	DMI	Breed	Sex	
-0.74	0.16	0.23	-	-	-	-0.06	0.02	0.72	Angus	Bulls and Heifers	Arthur et al., 2001a[b]
-0.54	**-0.08**	**0.48**	**-0.14**	**-0.08**	**-0.69**	0.01	0.03	**0.60**	Charolais	Bulls	Arthur et al., 2001b
-0.64	**0.29**	0.21	-0.08	**-0.40**	**-0.67**	0.01	0.03	**0.46**	Herford	Bulls and Heifers	Hennessy and Arthur, 2004
-0.63	0.07	**0.49**	**0.24**	-0.11	**-0.52**	-0.03	-0.02	**0.77**	Angus, Charolais, and hybrid crosses	Steers and Bulls	Nkrumah et al., 2004
-0.71	0.05	0.04	**0.29**	-0.11	**-0.50**	-0.02	-0.32	**0.62**	Crossbred[c] and Santa Gertrudis	Steers	Brown, 2005
-0.78	-0.08	0.03	**0.68**	-0.06	**-0.31**	0.00	0.01	0.16	Brahman	Heifers	Current Study

[a]Correlations in bold are different than zero (*P* < 0.05).
[b]Author did not include level of significance for correlations.
[c]Braunvieh-sired steers from four-breed rotational breeding (Angus, Simmental, Herford, and Braunvieh).

conversion ratio does not quantify the amount of feed used for maintenance, making it impossible to evaluate variation in the amount feed utilized for maintenance between animals (Arthur et al., 1996).

Partial Efficiency of Growth. Partial efficiency of growth (PEG), introduced by Kellner (1909) as cited by Nkrumah et al. (2004), is defined as the efficiency of weight gain per unit of feed intake available for growth (Hennessy and Arthur, 2004). Partial efficiency of growth is calculated as the ratio of ADG to DMI available for growth after accounting for maintenance requirements. The expected DMI available for growth is calculated as the difference in actual DMI and expected DMI for maintenance (Arthur et al., 2001a). High PEG is a desirable phenotype for this measure, indicating that the animal had a greater amount of gain per unit of available energy for gain after maintenance requirements are accounted for. Much like FCR this measure also has some potential problems associated with it. Estimation of maintenance requirements are not always reliable because of assumptions that are made when predicting the feed use for maintenance between animals (Archer et al., 1999). However, this method is a more attractive measure of efficiency because it takes into account the variation in energy required for both maintenance and growth between animals (Hennessy and Arthur, 2004). The correlation between ADG and PEG has been found to be from no different than zero (Hennessy and Arthur, 2004) to a correlation of 0.24 (Nkrumah et al., 2004). The partial correlation of PEG to ADG observed may be explained by the feeding standards used to calculate expected feed intake for maintenance (Nkrumah et al., 2004).

These authors also report negative correlations between DMI and PEG (Nkrumah et al., 2004; Hennessy and Arthur, 2004).

Residual Feed Intake. Koch et al. (1963) were the first to identify the potential use for residual feed intake (RFI) as an alternative measure of feed efficiency in cattle, in an attempt to partition feed into growth and maintenance components. They suggested that the efficient use of feed was not a directly measurable trait, but was a function of feed consumed, BW gain, and the time required to reach a certain point in production. Residual feed intake is defined as the difference, or residual between an animal's actual feed intake and the expected intake based on requirements for production and maintenance of BW, at a given level of production. The result of this measure of efficiency describes net feed conversion efficiency (Arthur et al., 1996). Deviation from their expected intake allows the determination of more or less efficient animals by the residual. Cattle that have a low RFI or negative residual, meaning they consumed less feed than expected for their body size and level of production (body weight gain), are more efficient. Less efficient animals have a positive residual or high RFI, meaning that they consumed more feed than expected for their body size and level of production, making them less efficient (Arthur et al., 1996; Archer et al., 1999). Residual feed intake is an attractive production tool because it is phenotypically independent of ADG and BW (Archer et al., 1999). This has been supported by several studies showing that RFI was independent of the production traits used to calculate it (Arthur, et al., 2001 a and b; Carstens et al., 2002; Nkrumah et al., 2004). Nkrumah et al. (2004) also showed in their study that RFI was independent of age. These findings suggest that selection based on

RFI should not change these production traits over time. In these studies, as would be expected, dry matter intake (DMI) was highly correlated with RFI. Residual feed intake has been shown to be moderately heritable in numerous studies (Koch et al., 1963; Fan et al., 1995; Pitchford, 2004). Koch et al. (1963) obtained a mean heritability of 0.28 ± 0.11 in the original investigation of RFI using growing bulls and heifers of British beef breeds. Fan et al. (1995) obtained a mean heritability of 0.14 for RFI in his study of growing Angus and Herford cattle. Herd et al. (2003) found that RFI in steers following divergent selection for post weaning RFI was independent of initial BW and ADG, but that actual feed intake was correlated with RFI (r = 0.50, $P < 0.001$) in the feedlot. These findings give support to the genetic potential that RFI may have in increasing performance through selection.

Predicted DMI is determined by a linear regression model. Regressions of weekly body weights are performed to determine ADG and mid-test metabolic BW ($MBW^{0.75}$). Predicted DMI is then determined by regressing actual DMI on ADG and $MBW^{0.75}$. Residual feed intake is determined as the difference or residual between actual DMI and predicted DMI (Arthur et al., 1996). Fan et al. (1995) discussed an alternate method for predicting intake using the National Research Council (NRC, 1984) to determine net energy requirements. This method uses animal weight, weight gain, and the nutrient content of the diet to estimate intake. However, this method of predicting intake has had some problems. In a study by Liu et al. (2000), looking at feed efficiency in young bulls, the NRC over predicted energy requirements for those animals. Intake was over predicted because these bulls were more efficient than the NRC standards predicted them to be. Utilizing this method, Fan et al. (1995) and Liu et al. (2000) found RFI to be correlated with BW and rate of gain. These findings indicate that the use of linear regression is a more appropriate means of estimating DMI for determining RFI.

Test duration is an important component of RFI evaluation. It has been shown that increasing the duration of the observation period for a particular trait will decrease the variation in that trait reducing the error associated with the measurement (Archer and Bergh, 2000). To obtain an RFI measurement, animals must be fed and data collected on an individual basis, for long periods of time. The economic requirements needed to evaluate animals for RFI, is one of the major limitations for its use as a production tool. Archer et al. (1997) assessed optimum test duration for ADG, DMI, and RFI in Angus, Herford, and Shorthorn cattle (Table 1.3). Based on their results, they determined that a minimum test length of 70 d was required to minimize variability in ADG with a reasonable level of confidence. It was determined that the variation in daily feed intake did not improve following d 35. This study also indicated that following d 70 there was little decrease in the variation of RFI. Accuracy of measurements decreased when BW estimates were taken greater than two weeks apart. As would be expected, increasing the number of measurements taken decreases variability. Wang et al. (2006) supported Archer and colleagues findings for length of test for DMI, but reduced the necessary length of test for ADG and RFI to a 63-d test utilizing *Bos taurus* crossbred steers. Archer and Bergh (2000) assessed the affect that biological type of cattle played on necessary length of test duration. They found that a 70-d test was sufficient to determine RFI in Afrikaner, Angus, and Simmental, but 84-d were required for Bonsmara and

Table 1.3. Recommended duration of feed efficiency evaluation

ADG	DMI	FCR[a]	RFI[b]	Breed	Sex	
70 d	35 d	70 d	70 d	*Bos taurus*	Bull, Heifers	Archer et al. (1997)
42 d	56 d	70 d	70 d	Afrikaner	Bull	Archer and Bergh (2000)
42 d	56 d	70 d	70 d	Angus	Bull	
42 d	56 d	84 d	84 d	Bonsmara	Bull	
42 d	56 d	84 d	84 d	Hereford	Bull	
56 d	79 d	70 d	70 d	Simmental	Bull	
63 d	35 d	42 d	63 d	*Bos taurus*	Steers	Wang et al. (2006)

[a]FCR = Feed intake required to produce one unit of weight gain.
[b]RFI = Difference in expected DMI for maintenance and growth at a given level of production and actual DMI.

Hereford cattle. These results are similar to those found by Archer et al. (1997) indicating that 70-to-84-d is an appropriate length to evaluate RFI. Archer and Bergh (2000) found that 56-to-70-d was required to accurately determine DMI, and 42-to-56 d was required to stabilize ADG across the same breeds. These results are longer than those reported by Archer et al (1997) with Simmental cattle being the reason for the increase in the upper limits. The amount of resources required to accurately obtain this measure is one of the major limitations to its use.

Genetic markers have recently been identified, and are commercially available (Bovigen, LLC, 2007) for the identification of efficiency based on RFI. This new feed efficiency test utilizes four genetic markers that together identify as much as a 15% difference in daily feed consumption with no affect on gain (Bovigen, LLC, 2007). Bovigen, LLC reported a highly significant association between RFI and the genetic markers associated with increased feed efficiency.

Selection of Feed Efficiency Traits. There are many feed efficiency measures that are available for use in beef cattle. There is no magic measurement for feed efficiency, and not all measures are appropriate for all production settings. Some measures can lead to a genetic change in rate of gain and mature BW. Understanding potential outcome and responses to selection for a particular efficiency trait is important for matching the appropriate trait to the appropriate production setting. Selection based on a given feed efficiency trait should reduce feed intake, while not causing dramatic changes in ADG or mature BW (Carstens et al., 2002). Increases in BW over time could result in an increase in maintenance requirement for those larger animals. Several studies have looked at how RFI, FCR and PEG relate, and what affect they have on production traits in *Bos taurus* breeds of cattle. Dry matter intake has been shown to be correlated to RFI, PEG, and FCR (Arthur et al., 2001b; Nkrumah et al., 2004). Arthur et al. (2001a), Hennessy and Arthur (2004), and Nkrumah et al. (2004) have also reported that RFI and PEG are correlated to DMI, indicating that selection based on these measures will result in decreased DMI. These authors have also indicated that RFI is independent of ADG, indicating that selection for efficiency based on RFI will not alter growth. Hennessy and Arthur (2004) found that PEG was independent of ADG, but FCR was correlated to ADG. Arthur et al. (2001b) and Nkrumah et al. (2004) found both PEG and FCR to be correlated to ADG, but found FCR to have a stronger correlation than PEG. All three measures are reported to be correlated to one another, so any selection based on one measure should improve an animal's efficiency, to some degree, in all measures (Table 1.4; Arthur et al., 2001b; Hennessy and Arthur, 2004; Nkrumah, et al., 2004; Brown, 2005). Utilizing measures of feed efficiency that are not independent of the traits required to calculate them could result in a change in those traits through selection. Altering these traits may change the animals being produced over time. Due to their correlation, selection for efficiency based on RFI and PEG has been reported by these authors to have the least amount of affect on ADG, while having more influence on decreasing DMI. These findings indicate that RFI and PEG may be more appropriate measures of feed efficiency than FCR.

Table 1.4. Phenotypic correlations between measurements of feed efficiency in beef cattle[a]

	Arthur et al., 2001b		Hennessy and Arthur, 2004		Nkrumah et al., 2004		Brown, 2005		Current Study	
Trait[b]	PEG	RFI	PEG	RFI	PEG	RFI	PEG	RFI	PEG	RFI
FCR	**-0.52**	**0.57**	**-0.56**	**0.45**	**-0.83**	**0.62**	**-0.76**	**0.52**	**-0.88**	0.04
PEG	-	**-0.65**	-	**-0.79**	-	**-0.89**	-	**-0.87**	-	-0.16

[a]Correlations in bold are different than zero (*P* <0.05).

[b]FCR = Feed Conversion Ratio, PEG = Partial Efficiency of Growth, RFI = Residual Feed Intake.

Variation in body composition has reported between high and low RFI cattle. Carstens et al. (2002) reported a negative correlation with RFI and ultrasound measurements of 12th rib fat thickness (r = 0.22; *P* =.004) and rump fat thickness (r = 0.18; *P* = 0.02) in *Bos taurus* crossbred cattle. There were no correlations observed between RFI and ultrasound measurements of ribeye area or intramuscular fat in these crossbred steers. Herd et al. (2003) reported that high RFI *Bos taurus* cattle had greater fat depth over the ribs (11.6 ± 0.3 and 10.2 ± 0.3; $P < 0.05$) and rump (14.8 ± 0.4 and 13.1 ± 0.4; $P < 0.05$), determined by ultrasound measurement, than low RFI cattle prior to slaughter. Hot carcass rump fat thickness was also different between high and low RFI cattle (16.5 ± 0.5 and 14.9 ± 0.5; $P < 0.05$) following slaughter. These studies indicate that low RFI cattle may produce a leaner carcass than high RFI cattle.

Understanding the interaction between various measures of feed efficiency is important when making decisions on which measures are appropriate to use. Arthur et al. (2001b); Hennessy and Arthur (2004); Nkrumah, et al. (2004); Brown (2005) report strong correlations between PEG, FCR, and RFI in *Bos taurus* breeds of cattle. These correlations indicate that selection for efficiency in one trait should improve efficiency in all traits to some degree.

Sources of Variation in Residual Feed Intake on Pasture

Forage Intake. Understanding the relationship between an animal's intake on pasture and their intake in confinement feeding relative to RFI will help us better manage and select for animals of greater efficiency. The amount of digestible nutrients consumed by a ruminant on pasture is one factor that influences animal performance in this setting (Lippke, 2002). Residual feed intake identifies animals that eat more or less than the expected amount for their body weight and production needs (Kennedy et al., 1993). Herd et al. (1998) examined how Angus cattle previously ranked for RFI as young heifers shortly after weaning, performed on pasture as mature lactating cows. In their study, the more efficient low RFI cows had a 7% heavier BW than the inefficient high RFI cows (618.0 ± 16.0 kg and 577.0 ± 11.0 kg; $P < 0.05$). Forage intake (determined by alkane analysis) was not significantly different between the efficiency groups, but the low RFI cows were determined to be more efficient on the basis that they had larger BW than the high RFI cows. The more efficient low RFI cows did not require more forage to compensate for the increase in BW. Findings in this study suggest the possibility of a phenotypic association existing between RFI determined in confinement feeding, in young post-weaned heifers, and their performance on pasture as mature cows (Herd et al., 1998). Herd et al. (2005) reported that following divergent selection for high and low post-weaning RFI, steers from the low RFI line out performed high RFI steers in BW (418 vs. 409 kg; $P = 0.07$) and ADG (0.66 vs. 0.64 kg/d; $P < 0.05$) on pasture, prior to feedlot entry. These authors suggest that selection for low RFI may not decrease DMI on pasture, but may increase production (ADG) in those more efficient animals at a given level of DMI.

Determining actual forage intake on pasture is difficult, making it necessary to utilize indirect methods to estimate intake (Dove and Mayes, 1991). Measures, based on fecal dry-matter (DM) output and corresponding forage DM digestibility, as well as fecal organic matter (OM) output and forage OM digestibility give intake estimates that span a longer period of time. This provides information about the variation between individual animals in a group (Dove and Mayes, 1991). Total fecal collection and the use of markers to estimate fecal outputs are the two main means of determining intake (Lippke, 2002). Total collection, a direct measurement of intake, is quite labor intensive. This procedure also has the potential to disrupt the animal's normal behavior, making it somewhat impractical for grazing cattle. An alternative indirect means of estimating intake is the use of an inert marker. Intakes estimated by utilizing markers are determined by the ratio of consumed marker to the concentration of marker that is recovered in the feces. An estimate of diet digestibility can be calculated and used to determine DMI (Burns et al., 1994). Owens and Hanson (1992) defined a digestive marker as a reference compound used to monitor the chemical (hydrolysis and synthesis) and physical (flow) aspects of digestion. There are two basic types of markers available for use as digestive markers. Inherent or internal markers are those that make up some internal, indigestible component of a feedstuff such as acid insoluble ash, long-chain fatty acids, or lignin. External markers are those that contain some form of inert compounds, such as rare earth elements (Owens and Hanson, 1992). The ideal inherent indirect marker should be easily identified during analysis and should be indigestible in the digestive tract (Dove and Mayes, 1991). The use of markers to estimate forage intake have an advantage over other means, such as total collection. Samples can be collected discreetly, preventing the disruption of activities such as grazing, which can be decreased with increased handling of animals.

Grace and Body (1981) first suggested that the use of long-chain fatty acids found in fresh herbage could be utilized as an indigestible fecal marker. Mayes and Lamb (1984) suggest that perhaps long chain n-alkanes would be a better inherent digestive marker because they are more chemically inert and easier to analyze than long-chain fatty acids. Mayes et al. (1986) were the first to develop a means of determining intake using natural alkanes as an internal marker. Natural alkanes found in herbage species consist predominantly of odd carbon (C_{25}-C_{35}) chains. The most abundant are nonacosane (C_{29}), hentriacontane (C_{31}), and tritriacontane (C_{33}; Mayes et al., 1986). Mayes and Lamb (1984) showed that complete recoveries of consumed alkanes are not achieved, but recovery progressively increased as chain length increased. To overcome shortcomings in the recovery of natural alkanes, Mayes et al. (1986) suggested dosing animals with a known amount of synthetic even chain alkanes (C_{28}-C_{32}) that could result in an equal amount of incomplete fecal recovery. The use of dosed even chained alkanes to determine the ratio of alkane loss accounts for the error of incomplete recovery of natural odd chain alkanes (Dove and Mayes, 1996). Utilizing alkanes to estimate intake is an appropriate measure, if a representative sample of the diet is collected, and there are similar fecal recoveries of both the natural and dosed alkanes. This method allows for the estimation of intake in individual animals, making it possible to examine the variation between animals (Dove and Mayes, 1991).

One limitation to the use of alkanes to assess intake of forage by cattle on pasture, is the need for daily dosing of even-chained synthetic alkanes. There are numerous means of delivering the dose of synthetic alkanes that require handling of the animals, disrupting the natural behavior and causing stress that alters intake (Burns et al., 1994). The use of the controlled-release capsule (CRC) technology to administer synthetic alkanes eliminates the need for frequently handling animals to administer doses. Molina et al. (2004) showed the effect that animal handling had on DMI in their comparison of the CRC with a daily dosed gelatin capsule to administer alkanes. There was a significant difference in DMI between the treatment groups with the CRC cattle consuming more than the gelatin capsule group. This was believed to be due to the daily handling required to administer the gelatin capsule doses to those animals. This study showed that 5 d are required for the excretion of alkanes to reach a stable plateau with the CRC. There was no difference in the dosed alkane recovery between treatments, indicating both were effective in predicting intake. It was determined that the C_{33}:C_{32} alkane pair was the most accurate for estimating DMI in both methods. Dicker et al (1996) determined that when using the CRC that alkane concentrations stabilized from d 3-to-5, and continued to maintain stability until d 14-to-19 when they began to decline. Berry et al. (2000) explored the use of the CRC and a daily grab sample approach to estimate intake. They determined that 7 d of fecal collection were necessary to accurately estimate intake between d 8-to-14. Using less than 7 d of sampling tended to underestimate intake early in the sampling period and overestimate intake in the last days of the fecal sampling window. However, if samples were collected for 5 d between d 9-to-13 there was little reduction in the accuracy of intake estimation as opposed to a 7 d fecal collection.

Grazing Behavior. Differences in feeding patterns between high and low RFI animals have been observed in many species. This has contributed to the explanation of a portion of the variation between efficiency groups in those animals (Richardson et al., 2000). Richardson et al. (2000) evaluated the variation in activity for high and low RFI Angus bulls following one generation of divergent selection for RFI. They found no difference in the amount of time spent lying, standing, or walking between efficient and inefficient animals in confinement. Data from Angus steers, following one generation of selection, found that low RFI steers had greater intakes in a feeding session than high RFI steers (1.38 ± 0.11 kg and 1.16 ± 0.08 kg; *P* =. 0.09), but had fewer feeding sessions per day than high RFI steers (8.3 ± 0.7 and 10± 0.6; *P* = 0.07) in confinement feeding. Determining differences in the amount of time spent on the various grazing patterns of high and low RFI cattle may help explain differences in efficiency.

It is well established that *Bos indicus* cattle have a high level of heat tolerance, and are well adapted to warmer more humid environments. This increased tolerance to heat allows these animals to experience less heat related stress. Bennet, et al. (1985); Forbes et al. (1998); and Sprinkle et al. (2000) showed that Brahman and Brahman influenced cattle spent more time grazing during daytime periods of heat, and less time in the shade than Angus and Shorthorn cattle. Nighttime grazing times were not different for these breeds of cattle, indicating that heat stress was the limiting factor in daytime grazing.

Grazing is the primary means of nutrient intake for cattle on forage (Lippke, 2002). When forage availability is not limiting, bite size, biting rate, and time spent grazing are the behavioral activities that regulate forage intake in grazing animals. Using these activities as an indication of intake allows for the investigation into how variation between animals influences forage consumption (Erlinger et al., 1990). Various jaw movements are required for ruminants to physically consume and process herbage during ingestion and rumination. Observation of a particular jaw movement that is characteristic of a particular grazing activity allows a means of determining the amount of time spent on that activity (Ungar and Rutter, 2006). An animals grazing pattern consists of the time spent grazing, ruminating, and the down time between these activities. Penning (1983) constructed a transducer that was capable of recording jaw movements of grazing sheep. A computer program created a time line of events allowing measurement of grazing, ruminating, and idling time. Jaw movements caused stretching and contracting of a nose band that acted as a transducer creating an electrical signal that corresponded to jaw movements. The electrical signal created is then sent as an analog signal that is recorded by a cassette recorder carried by the animal. Penning et al. (1984) developed an algorithm that uses the characteristics of the waveforms produced by the alteration of electrical signals during jaw movement to differentiate between rumination and grazing activities. This allowed ruminating and grazing to be further partitioned into the number of bites and chews taken during the given activity. Rutter et al. (1997) further improved the Penning et al. (1984) system by replacing the analog recorder with a microcomputer-based system allowing digital recording of jaw movements. Data stored on a memory card can be taken from the device and uploaded onto a computer and analyzed by the Graze Analysis Program to identify individual jaw movements

(Ungar and Rutter, 2006). The Graze system allows for the visual observations of the characteristics associated with jaw movements by plotting the variation in amplitude created by the particular jaw movement against time (Rutter et al., 1997). Understanding variation in grazing behavior in animals of varying levels of efficiency (RFI) may help explain subsequent variation in intake by those animals.

Ungar and Rutter (2006) compared the use of the Institute of Grassland and Environmental Research (IGER) Behavior Recorder (IBR) method to the acoustic monitoring (ACM) method for recording grazing activity. The IBR system worked well when counting total number of jaw movements and subsequently determining bite rate (bites/min). The IBR system tended to overestimate the number of bites taken compared to the ACM system, which was thought to be related to the misclassification of sub-peaks. The IBR system matched the ACM system well when identifying pauses in the timeline between activities. This system was also able to detect bites that were taken without an accompanying chew or terminating bites when the ACM system could not. The IBR system tended to overestimate bite rate by about 24.6% because of the periodic misclassification of chews as bites. The misclassification of chews as bites was determined to be the major problem with the IBR system.

Many factors have an influence on grazing behavior in ruminants. Forbes and Coleman (1993) showed that an increase in green leaf and herbage mass resulted in an increase in grazing time. Chacon and Stobbs (1976) concluded that leaf yield was the most important sward component that dictated intake by grazing animals. They reported that in early stages of leaf defoliation that grazing time and bite rate increased, but in the late stages of defoliation these behaviors decreased in cattle. Erlinger et al. (1990) looked at the effect of mature size on grazing time, and reported that heifers with a larger body size spent more time grazing than heifers with a smaller body size.

Twenty-four hour grazing times for beef cattle are reported to range from: a mean of 632.5 ± 51 min/d for Hereford x Friesian and blue-gray cattle grazing a dense sward of perennial ryegrass, 776.5 ± 51 min/d for cattle grazing an open sward of perennial ryegrass (Forbes and Hodgson, 1985); 543.0-to-721.0 min/d for Herford x Angus cattle grazing Caucasian old world bluestem, 465.7-to-733.0 for Plains old world bluestem (Forbes and Coleman, 1993); and 348.0-to-515.0 min/d for 16-mo old *Bos taurus* heifers grazing summer Bermudagrass (Erlinger et al., 1990). Forbes et al. (1998) reported two primary grazing periods during daytime grazing (0700-to-1100 and 1700-to-2000) and that Brahman heifers grazed on average about 80-to-180 min and 170-to-190 min; respectively. Bite rate (bites/min) determinations have been reported to range from 62-to-65 bites/min for cattle grazing a dense sward of perennial ryegrass, 58-to-67 bites/min for cattle grazing an open sward of perennial ryegrass (Forbes and Hodgson, 1985), 36-to-57 bites/min for cattle grazing Caucasian old world bluestem, and 37-to-56 for Plains old world bluestem (Forbes and Coleman, 1993). Erlinger et al. (1990), observed an average of 30-to-47 bites/min in 16-month-old *Bos taurus* breeds of heifers grazing summer bermudagrass.

Biological Variation in Residual Feed Intake

Digestive Kinetics. Rate of digesta flow through the digestive tract of a ruminant plays an important role in determining the site where digestion occurs. Starch is the highly digestible product that is found in grain sources fed to growing cattle (Huntington et al., 2006). Owens et al. (1986) determined that more energy could be provided as a result of starch and non-fibrous carbohydrate digestion in the small intestines as opposed to the rumen. Starch that is digested in the small intestine is catabolized into glucose and absorbed in the small intestines (Huntington et al., 2006).

Digesta flow markers are used to determine the rate at which food particles move through the digestive tract. Fecal recovery of external markers attached to particulates of a dosed meal, allows for the calculation of passage rate. Determining passage kinetics using marked feed is an extremely sensitive measurement. Cattle have a large digestive capacity with relatively slow turnover making it difficult to follow the small amount of marked feed through the digestive tract (Pond et al., 1985). Rare earth elements (Ytterbium) make ideal external markers as they are metabolically inert, indigestible, and remain attached to food particles through normal rumen pH conditions (Ellis et al., 1994).

Pulse-dosing of a marker allows for the estimation of pool size and dilution rates in the digestive tract. Evaluating the rate of decline in fecal concentration of the marker gives an estimate of dilution rate, pool size, and lag time (Owens and Hanson, 1992). Ellis et al. (1994) reviewed the methodology of estimating digestive kinetics, describing the flow of digesta through the segments of the digestive system of the ruminant. Consumed forage undergoes various chemical and mechanical alterations as it moves through the digestive tract. Ellis et al. (1994) described a two-compartment model (CMS) consisting of age-dependent (CM1) and age-independent (CM2) compartments.

The CM1 compartment is a lag compartment that gives forage particles the necessary conditioning time required prior to their eligibility for escape (Forbes et al., 1998). The longer the particles reside in this compartment the greater the opportunity for their escape. Gamma functions allow for adjusting the age-dependent rate parameter, λ (Pond et al., 1988). The CM2 compartment represents the constant rate of particle turnover, resulting from the mixing of an influx of particles with the resident particles in the compartment. This compartment maintains a constant volume with the influx of particles equaling the efflux of particles, giving all resident particles opportunity for escape (Ellis et al., 1994). Other secondary measures of kinetics include the age-dependent age-independent mean compartmental residence time for the system (MCRTS). Also referred to as the turnover or clearance time, MCRTS is a measure of the mean time that dosed particles reside in both compartments before escape. The time delay between dosing and first detection of marker (TAU) represents the residence time associated with passage of marker through the intestines. Gastrointestinal residence time (RTG) is the sum of the MCRT and TAU. Fecal output (FO) is estimated by the dilution of dosed marker recovered from the collected feces. Timing and duration of fecal collection is essential for accurate estimations. Optimal timing of fecal samples requires the collection of samples prior to anticipated appearance of marker to establish a baseline, two-to-four samples during the ascending phase of the marker concentration profile, and more widely spaced samples during the decline of the marker concentration profile (Ellis et al., 1994 and Forbes et al., 1998).

Dry Matter Digestibility. Variation in dry matter digestibility (DMD) could potentially explain some of the subsequent variation in RFI. Animals with an increased ability to digest their diet would be expected to perform better than animals with average or less than average digestibility. Digestibility can be altered by level of intake relative to maintenance requirements, but more importantly genetic variation in total tract digestibility may be responsible for variation (Herd et al., 2004). Richardson et al. (1996) investigated the variation in DMD in British heifers and bulls during the RFI evaluation period. Although not significant, low RFI animals had a tendency to digest their feed 1% better than the high RFI animals. This difference does not seem large enough to be important, but these authors show that this small difference equates into a 2.3% decrease in daily feed required for a 450 kg calf gaining at 1.3 kg/d with a diet representative of their study (69% DMD). This study revealed that there was an average of 16% difference in DMI between the high and low RFI animals in this study. Of the 16% difference in DMI, 2.3% can be attributed to difference in DMD, equating to a 14% explanation of variation in DMI (Richardson et al., 1996). Richardson et al. (2004) also found no significant difference in DMD between efficiency groups in steers following one generation of divergent selection for RFI. In their study DMD had a negative correlation with RFI in an animal housing period ($r = -0.44$; $P < 0.05$; a metabolic assessment portion of their experiment), but was not significantly correlated with RFI over the entire experiment. Brown (2005) found that DMD was negatively correlated ($r = -0.32$, $P < 0.05$) to RFI in growing steers, equating in a 6.6% difference in digestibility from high to low RFI. A negative correlation would mean that more efficient animals would digest their rations better than the less efficient animals. These studies indicate the possibility that variation in DMD, although small, may help explain a proportion of the variation in RFI.

Sales and Janssens (2003) review a method of determining digestibility by utilizing the acid insoluble component of feedstuff as an internal marker. Shrivastava and Talapatra (1962) were the first to introduce the use of acid-insoluble residue as an indication of digestibility. Their findings revealed that fecal recovery of the residue was satisfactory, and digestibility calculations agreed fairly well with the conventional methods (Cr_2O_3). Van Keulen and Young (1977) support these findings by showing satisfactory estimations of DMD. In this study diurnal variation was explored in sheep by taking fecal samples every 2-h for a 24-h period. They found no significant difference in the recovery of AIA in the feces, even following ration removal, indicating that there is no diurnal pattern in the excretion on AIA in the feces making it possible to collect samples at any time of the day in sheep under conditions similar to their study. Internal markers are the natural indigestible components found within feedstuff (Kotb and Luckey, 1972). Acid insoluble ash is measured as the residual following the complete ashing of acid detergent fiber residue (ADF; Van Soest et al., 1991). The resulting product of AIA is the indigestible mineral components (silica) in the feedstuff (Sales and Janssens, 2003). Digestibility is determined by the ratio of known AIA in the diet, and the known amount recovered in the feces (Burns et al., 1994). An alternative to total collection, AIA allows for the use of a grab sample, if multiple samples are collected over a period of time (Van Keulen and Young, 1977; Sales and Janssens, 2003).

Temperament. Animal temperament has a negative impact on numerous aspects of beef cattle production such as; BW gain (Voisinet et al., 1997b), milk production (Breuer et al., 2000), carcass tenderness, and the occurrences of dark-cutters (Voisinet et al., 1997a). Temperamental cattle are those that easily become excited and agitated when handled in a confined area or a stressful situation, such as a squeeze chute or a crowding pen (Voisinet et al., 1997a; Voisinet et al., 1997b). Von Borell (2001) defines stress as the result of internal or external stimulation that causes a deviation from homeostasis. Temperamental animals not only have reduced performance because of there temperament, but they can also be dangerous to handle and hard on equipment. Exit velocity (EV), developed by Burrow et al. (1988), is an objective means of measuring temperament in beef cattle. Exit velocity is a measurement of the rate at which an animal exits a stressful situation such as a squeeze chute. Curley et al. (2006) defines an appropriate tool to measure temperament in beef cattle as one that must be reliable, repeatable, and indicative of an individual animal's reactivity to stressful situations. Exit velocity is an attractive tool to access temperament in beef cattle because there is no human bias in its measurement, it is repeatable, and it measures individual responsiveness. Tǒzsér et al. (2005) in their comparison of EV and the chute score (a subjective measure of temperament) support the repeatability of EV as a measure of temperament and its lack of discrimination based on human observation. When cattle are exposed to stressful situations an adrenal response takes place. The central nervous system, immune system, and endocrine system all interact in response of the stressor (von Borell, 2001). The hypothalamic-pituitary-adrenocortical axis is responsible for producing the many hormones that are responsible for the response to stressors. Cortisol concentrations in the blood are used as indicators of stress response in animals (Möstl and Palme, 2002). Exit velocity has been reported to be positively correlated to serum cortisol concentrations in cattle, indicating that it is an accurate tool for evaluating temperament (Fell et al., 1999; Curley et al., 2006). Curley et al. (2006), investigating the interaction of EV over time, reported that EV decreased over time, but individual animal rank did not change over time. Exit velocity decreased significantly from d 0-to-120. Day-zero was found to be significantly higher than d 60 (mid-test point), but no difference was seen from d 60-to-d 120. Fell et al. (1999) when looking at the relationship of EV at weaning and in the feedlot, found no significant differences in EV between the two time periods. These studies suggest that EV may change over time, but rank will remain relatively constant. Fell et al. (1999) also observed in this study that the weaning process did not play a role in changing EV rank. Research shows that temperament has a significant impact on cattle performance in confinement feeding. Calmer animals, or those with a slower EV, have been shown to have a higher ADG than animals with an excitable temperament, or rapid EV (Burrow and Dillon, 1997; Voisinet et al. 1997b). Petherick et al. (2002) did not see a significant difference in ADG between EV grouped cattle in the feedlot, but did observe a tendency for the calm animals to gain more. Total pen feed intakes did not differ in these cattle sorted and fed by EV. Variation in production traits caused by variation in temperament could also cause variation in feed efficiency. Richardson et al. (2000) saw no difference in EV in the first generation progeny of high and low RFI cattle. Fox (2004) and Brown (2005) found that in growing bulls and growing and finishing steers that EV did not have an effect on RFI, but that it was negatively correlated with ADG, BW and DMI.

Conclusion

There is a large cost incurred by producers when providing feed and forage to beef cattle. In order to maximize profitability, producers must select for those animals that will most efficiently utilize feedstuffs provided. There are many measures of feed efficiency available to help identify animals of varying levels of efficiency. Historically, FCR has been used to select efficient animals. Although, selection based on this measure does improve feed utilization, it may eventually have a negative impact on production due to its association with the performance trait, ADG. Increasing ADG through selection has the potential to increase mature BW. This emphasizes the need to study other measurements of efficiency that will have less potential to increase mature BW. Identifying and understanding the sources of variation that exist between animals of varying levels of efficiency is important. Having a better understanding of these sources of variation will help producers select and better manage efficient animals. Residual feed intake identifies animals that eat less than expected for their given level of production, without limiting their production. RFI is an attractive production tool because it is independent of ADG and BW, thus selection for efficiency based on RFI should not increase animal size or maintenance requirements. RFI is a moderately heritable trait, and making selections based on RFI should increase efficiency in future generation. Understanding how the association of RFI determined in confinement feeding relates to animal performance on pasture will help us to select cattle that will be more efficient in both production settings.

CHAPTER II

SOURCES OF VARIATION IN RESIDUAL FEED INTAKE AND HOW IT RELATES WITH OTHER MEASURES OF FEED EFFICIENCY

Introduction

Providing feed to livestock is a major contributor to the cost associated with production. The increase in the use of agricultural feedstuffs as a source for producing "alternative" energy is becoming, and will continue to be, a major issue for beef cattle producers. The high cost associated with feeding livestock makes this one area that can have a significant effect on a producer's profitability. The cost of providing feed or forage to livestock is an inevitable part of livestock production. Therefore, selection must be made to identify animals that efficiently utilize those feedstuffs provided to them, in order to maximize profitability. There are many feed efficiency traits used to measure feed efficiency in beef cattle production. Selecting for feed efficiency should not result in an increase in mature BW, which could have a negative impact on production. A good measure of feed efficiency must be one that accounts for both variations in energy required for maintenance and gain, among individual animals (Arthur et al. 1996). Feed conversion ratio (FCR), is perhaps the most common measure of feed efficiency utilized in beef cattle production (Archer et al., 1999; Nkrumah et al., 2004). Efficiency based on FCR is calculated as the ratio of feed intake to BW gain (Arthur et al., 1996; Arthur et al., 2001a). Efficient animals with a low FCR are considered to be more efficient because they require less feed to produce a unit of gain, while animals with a high FCR require more feed to produce that same unit of gain. A second measure of feed efficiency, partial efficiency of growth (PEG), is defined as the efficiency of weight gain per unit of feed intake available for growth (Hennessy and Arthur, 2004). It is calculated as the ratio of ADG to expected DMI available for growth. The expected DMI available for growth is calculated as the difference in actual DMI and expected DMI for maintenance (Arthur et al., 2001a). An efficient animal would have a high PEG, indicating that they produced a greater amount of gain per unit of available energy for gain, after maintenance requirements are accounted for. This is a more attractive measure of feed efficiency because it takes into account the variation in energy required for both maintenance and growth between animals (Hennessy and Arthur, 2004). Residual feed intake (RFI) is a measure of feed efficiency that identifies animals that consume less feed than expected for their given level of production, without having an affect on their level of production. Residual feed intake is determined as the residual between actual DMI and predicted DMI (Arthur et al., 1996). Efficient animals based on RFI are those that have a negative residual, low RFI, indicating that they consumed less feed than what would be expected for their given level of production. Inefficient animals would consume more than expected resulting in a positive residual or high RFI.

Physiological differences have been noted between efficient and inefficient animals. Understanding the causes for these differences between animals of varying efficiency will help us select and better manage efficient beef cattle. These sources of variation between cattle of varying levels of efficiency may potentially be used as an indicator to better help identify an animal’s efficiency in a production setting.

Knowledge of a given animal's level of efficiency may allow a producer to make better decisions on how to market and manage that animal. The objectives of these experiments are to examine the phenotypic relationship between different measures of feed efficiency and to determine and characterize sources of variation in RFI in growing Brahman heifers.

Materials and Methods

Three separate 70-d feeding trials were conducted on three separate groups of Brahman heifers. Individual performance and feed intake data were collected in order to determine variation in feed efficiency. Apparent DMD, digestive kinetics, and temperament data were collected to determine if physiological differences occur between animals of varying efficiencies.

Experiment I. Brahman Heifers (n = 31; 16-to-19 mo of age) from the spring 2004 calf crop were used in a 70-d feeding trial, during the fall of 2005, in a Calan gate system (American Calan, Northwood, New Hampshire) at the Texas Agricultural Experiment Station (TAES), Overton. Heifers were fed a pelleted 12% crude protein (CP) receiving ration (Table 2.1) at 2.2% of their gross body weight 7 d prior to entering the Calan gate system. Upon entry, heifers were assigned a pen based on weight and fitted with an electronic key, worn around their neck, which allowed them access to their respective feed bunk in the Calan gate system. Animals were given a 4-d training period to teach them to eat from the Calan gates, and allow for removal of animals that would not eat from the stanchions. On the first day, gates were fixed in the open position so that heifers could locate the feed in the stanchions. The following 2 d gates were allowed to

Table 2.1. Ingredients and nutrient content of experimental diets

	Experiment	
Diet	I and II	III
Ingredients (As-fed-basis):		
Cotton seed hulls	25.00	37.50
Soy hulls	20.00	-
Corn, ground	10.00	6.37
Alfalfa dehy 20%	8.73	12.50
Wheat midds	7.35	5.53
Rice bran	6.25	8.50
Cottonseed meal 41	6.01	4.33
Corn gluten feed	5.00	5.00
Corn, cracked	5.00	5.00
Binder molasses	2.00	2.00
Calcium	1.25	1.27
Whole cotton seed	0.93	-
Salt	0.62	0.67
BIOFOS 21P 18CA	0.56	0.51
Soybean meal	0.50	4.75
Dynamate	0.26	0.25
BGY 28	0.25	0.25
Xtra-bond	0.15	0.15
T/M for dairy	0.05	0.05
Dairy (ADE)	0.04	0.04
Vitamin A-30	0.04	0.04
Zinpro	0.03	0.03
Equine T/M	-	0.01
Rice hulls	-	5.25
Nutrients (Dry-matter-basis):		
DM, %	90.33	90.24
CP, %	13.40	13.41
NE_m, Mcal/kg	1.59	1.41
NE_g, Mcal/kg	0.90	0.68
ADF, %	34.36	38.17
NDF, %	48.34	51.23
Calcium,%	1.00	1.00
Phosphorus,%	0.55	0.55

close, but the latches were secured open with tape so that the heifers could learn that applying pressure to the gate would open it. On the final 2 d, tape was removed from the latch so that the heifers could find their designated stanchion, and learn to operate the gate with their electronic key. Six heifers were removed from the trial on d 0 (start of test) because they were unable to learn how to eat from the Calan gates. On d 0 body weights were determined and feed allocation for each heifer was calculated (2.2% BW) for that week. Heifers were fed their ration once daily in the morning (0800 h). Weekly BW was determined and daily feed allocation was adjusted for the following week based on the new BW (2.2% BW). Body weights were taken on the first d of each new week in the morning prior to feeding. Weekly orts (if any) were collected and weighed at the end of each week, following BW determination, to adjust actual feed intakes for the previous week. Each heifers daily feed allocation for the new week was weighed out into separate feed sacks (seven per animal), and stored in a container in front of the animal it corresponds to so that daily ration could be easily fed. Weekly fecal samples were collected from the rectum of each animal at each weighing, from d 0-through-70 to determine acid detergent insoluble ash (ADIA) concentration. Samples were stored in individual, labeled, freezer-bags, and frozen at -20° C for later analysis. High (n = 4) and low (n = 4) RFI heifers were evaluated for digestive kinetics on d 77. Heifers were maintained on the same diet, fed at the same rate, throughout the entire experiment. Two heifers were excluded from the trial and any subsequent analysis due to persistent bloating problems during the feeding trial. At the end of the 70 d experiment, 23 were available for further evaluation.

Experiment II. Experiment II, spring 2006, was conducted exactly as Exp. I. In Exp. II, Brahman Heifers (n = 50; 10.5-to-13.5 mo of age) from the spring 2005 calving season were used in a 70-d feeding trial in the Calan gate system at the Texas Agricultural Experiment Station, Overton. Heifers were fed the same ration as in Exp. I at 2.2% gross BW. Weekly fecal samples were collected, as in Exp. I, for analysis. High (n = 6) and low (n = 6) RFI heifers were evaluated for digestive kinetics on d 77. Heifers were maintained on the same diet, fed at the same rate, throughout the entire experiment. Ten heifers were removed on d 0 because they were unable to learn how to use the Calan gates. At the end of the trial 39 heifers successfully completed the entire trial and were available for evaluation of feed efficiency and apparent DMD.

Experiment III. Experiment III, fall 2006, was conducted similarly to Exp. I and II. In Exp. III, Brahman heifers from the spring 2006 calf crop (n = 56; 5-to-8 mo of age) were used in a 70-d feeding trial in the Calan gate system at the Texas Agricultural Experiment Station, Overton. Heifers were fed a 12% CP receiving ration (Table 2.1) at 2.5% of their BW daily. High (n = 8) and low (n = 8) RFI heifers were evaluated for digestive kinetics on d 77. Heifers were maintained on the same diet, fed at the same rate, throughout the entire experiment. Twelve heifers were removed from the trial by d 0 because they were unable to learn how to eat from the Calan gate system. One heifer was removed on d 35 because she was severally bloated and went off feed. Two additional heifers were removed when they went off feed. At the end of the trial 41-heifers successfully completed the entire trial and were evaluated for feed efficiency and digestive kinetics.

Determination of Feed Efficiency. Following each 70 d feed efficiency evaluation, heifers were ranked based on RFI by determining the residual between the actual and expected DMI for each heifer. Expected DMI was determined by linear regression of actual DMI, ADG, and mid-test $BW^{0.75}$. A 3% shrink was applied to all weights in order to achieve a shrunk body weight (SBW). Weekly SBW was regressed against day for each animal, and the slope of the regression line was used to determine the ADG for that animal. The intercept of the regression line was used as the d 0 or initial SBW. The slope of the line and the intercept were used to calculate the d 70 or final SBW. Mid-test weight was determined by taking the average of the initial and final SBW determined by the regression equation. Mid-test metabolic BW ($BW^{0.75}$) was calculated as the mid-test SBW to the power of 0.75. Heifers were ranked based on the residual and assigned to high (residual > ½ standard deviation above the mean), medium (residual is ± ½ standard deviation from the mean), or low (residual < ½ standard deviation below the mean) RFI groups within each experiment. Feed conversion ratio was determined by taking the ratio of DMI to ADG (FCR = DMI kg ÷ ADG kg). Partial efficiency of growth was determined by the ratio of ADG to DMI available for growth. The DMI available for growth is the residual, after the expected DMI for maintenance had been accounted for in the actual DMI. Expected DMI for maintenance was determined by $0.077 \times BW^{0.75} \div NE_m$ concentration of the diet (NRC, 2000).

Digestive Kinetics. On d 77 of feeding, following the 70 d feed efficiency evaluation, heifers were pulse dosed with 150 g DM Ytterbium chloride (Yb) labeled to Tifton-85 Bermudagrass hay for determination of digestive kinetics using the pulse dose marker technique (Burns et al., 1994). Heifers were maintained on the experimental diets with the same level of intake as described in the feed efficiency evaluation throughout the digestive kinetics evaluation. Residual feed intake was calculated following the 70 d feed efficiency evaluation using the actual performance data to identify the most and least efficient heifers, based on this means of calculating RFI. In Exp. I, 4 high and 4 low RFI heifers were dosed, and in Exp. II and III 6 high and 6 low RFI heifers were dosed. When RFI was calculated using the regression line of weekly BW to calculate performance traits, rank was affected, causing some of the heifers to move into the medium RFI group. Only heifers with a high and low RFI were utilized to evaluate the variation in digestive kinetics between the efficiency groups. In Exp. I (4 high and 2 low RFI) and III (2 high and 3 low RFI) the dose was combined with daily ration, and refusals were collected to determine actual dose intake. In Exp. II (5 high and 3 low RFI) heifers were gavaged with the dose in the afternoon (~ 1600 h). On d 78 starting at 0700 through 1800 h all defecations from dosed animals were sub-sampled. On d 79 three fecal samples were collected at 0700 h, 1200 h, and 1800 h. On d 80 and 81 fecal samples were collected twice daily at 0900 and 1500 h. A final fecal sample was collected on d 82 at mid-day (1200 h). All fecal samples were frozen and stored at -20° C for later Ytterbium analysis.

To determine Ytterbium concentration, fecal samples were dried at 100° C, ground to pass a 1-mm screen. Ytterbium was extracted from 0.2 g of sample, and the concentration was determined by atomic absorption spectroscopy (Hart and Polan, 1984). Estimations of passage kinetics were calculated using a two compartment, gamma

2 residence model as described by Ellis et al. (1994). The following secondary variables were calculated as describes by Ellis et al. (1994) two compartment model: the age-independent turnover (CM2), an age-dependent compartment residence time (MCRT) which provides the lag time necessary for the conditioning of feed particles prior to their escape from the compartment, age-dependent age-independent compartment residence time (MCRTS), gastrointestinal residence time (RTG), the initial time delay before the detection of the marker (TAU), and fecal output (FO).

Fecal VFA. Fecal samples were collected from the rectum of each animal (Exp. I, n = 23; Exp. II, n = 12; Exp. III, n = 13) determine variation in fecal VFA profile between the efficiency groups. A single fecal sample was collected on d 81 and d 82 for Exp. I, and d 82 for Exp. II and III. Approximately 10 g of fresh feces was mixed with 20 ml deionized water and vortexed. An aliquot (8 ml) of this mixture was pipetted into a vial containing 2 ml of 25% metaphosphoric acid and frozen. Gas chromatography was used to identify and determine VFA concentration (Sindt, et al., 2002).

Apparent DM Digestibility. To determine variation in apparent DM digestibility, acid detergent insoluble ash (ADIA) was used as an internal marker to predict fecal output for heifers in Exp. I and II. Based on actual intakes and predicted fecal output apparent DM digestibility was estimated for each heifer in Exp. I and II. Fecal samples were collected once weekly from each animal throughout the RFI evaluation periods and used for ADIA analysis. Feed samples were collected from each bag of feed when individual daily rations were weighed out each week. Samples from each sack were combined to make a composite sample for each wk (10 composite samples per excitement). Samples were dried at 60°C and ground to pass a 1mm screen. Acid detergent insoluble ash was determined by the change in weight created by completely combusting the ADF portion of the samples (Van Soest et al., 1991). Acid detergent fiber content of samples was determined using an ANKOM Fiber Analyzer (ANKOM Technology, 2005). Pre-weighed fiber analysis filter bags were filled with approximately 0.5500 to 0.6500 g of feces and dried at 60°C for 48 h to obtain a DM weight. Samples were then placed in an ANKOM Fiber analyzer and washed in an ANKOM ADF solution for 1 h at 100°C. Following the wash, samples were rinsed in boiling distilled water (100°C) 3 times for 5 min each, and then placed in a beaker of acetone for 5 min. Following the rinse cycle, samples were dried in an oven for a minimum of 2 h at 105°C and weight was recorded. Weighed samples were then placed in a pre-weighed Pyrex beaker and ashed in a muffle furnace at 525°C for 6 h. Samples were given time to cool in desiccators with desiccant for 1 h and final ash weight was determined. Weekly digestibility values that were greater than 100% and less than 0%, are not biologically possible, and were removed from analysis. Weekly DMD were averaged to determine overall DMD for each animal.

Temperament. Temperament was measured at weaning on each animal in all three experiments using an objective measure, exit velocity (EV), and a subjective measure, pen score (PS). Individual animals were assigned a pen score (Kunkle et al., 1986) based on visual assessment of how they react while confined to a pen with a small group of cattle (n = 3-to-5). Pen score is based on a 1-to-5 scale, with a score of 1 representing a calm animal that is non-aggressive, moves slowly, can be approached, and is not excited by the presence of humans. A score of 5 represents a very aggressive extremely excitable animal that runs into anything in its path, and is aggressive towards humans. Exit velocity (Burrow et al., 1988) is the measure of the rate (m/s) at which an animal exits a squeeze chute and travels 1.83 m (Curley et al., 2006). Measures of temperament were taken at weaning in all three groups of animals. Each animal was then given a temperament score (TS), determined by the mean of the EV and PS for each animal [TS = ((EV+PS)/2)].

Statistical Analysis. Heifers and their respective RFI ranking, assigned during the individual experiments, were pooled across all three experiments for analysis. Least squares procedures using PROC MIXED of SAS (SAS Inst. Inc., Cary, North Carolina) were used to examine the effects of RFI group on performance, efficiency, fecal VFA concentration, DMD, and temperament measurements. The model included RFI group as a fixed effect and experiment as a random effect. Least squares procedures using PROC GLM of SAS were used to examine the effect of RFI group on digestive kinetics. The model included RFI as the class variable and passage kinetic parameters as the dependent variable. Differences in RFI groups were determined by the F-tests using type III sums of squares. The PDIFF option of SAS was used for mean separation. Partial correlation coefficients among traits were determined by PROC CORR of SAS.

Results

Summary statistics for each group of heifers evaluated are presented in Table 2.2. Brahman heifers averaged 11.2 (SD = 4.08) mo of age, and had an overall initial BW of 241 kg (SD = 47), a final BW of 288 kg (SD = 53), MBW$^{0.75}$ of 64.9 kg (SD = 9.5), and

Table 2.2. Summary statistics of traits measured in three experimental trials in growing Brahman heifers[a]

	Exp. I	Exp. II	Exp. III
Number of heifers	23	39	41
Age, mo	17.4 ± 0.64	12.0 ± 0.82	7.0 ± 0.64
Residual feed intake, kg/d	0.00 ± 0.31	0.00 ± 0.03	0.00 ± 0.06
Initial BW, kg	309 ± 27	241 ± 28	204 ± 23
Final BW, kg	354 ± 30	297 ± 34	243 ± 29
Mid-test metabolic BW, kg	77.6 ± 4.9	66.1 ± 5.55	56.6 ± 5.02
ADG, kg/d	0.66 ± 0.13	0.79 ± 0.15	0.55 ± 0.14
DMI, kg/d	7.3 ± 0.72	6.2 ± 0.71	5.5 ± 0.64
Feed conversion ratio, DMI:ADG kg	11.45 ± 2.59	7.91 ± 1.31	10.65 ± 3.29
Partial efficiency of growth, ADG:DMI growth	0.19 ± 0.04	0.27 ± 0.04	0.23 ± 0.05
Exit velocity at weaning, m/s	1.96 ± 1.30	2.95 ± 1.63	2.38 ± 0.91
Pen score at weaning	2.83 ± 1.37	2.97 ± 1.30	2.43 ± 0.93
Temperament score at weaning[b]	2.38 ± 1.26	2.96 ± 1.13	2.41 ± 0.82

[a]Data is reported as mean ± SD.
[b]Temperament score = average of pen score and exit velocity.

Table 2.3. Difference in performance, feed efficiency traits, and measurements of temperament for Brahman heifers evaluated for RFI

Trait	Mean[b]	SD[c]	RFI group[a]			*P*-Value
			High	Medium	Low	
Number of Heifers			36	33	34	
Initial BW, kg	241	47	253 ± 31	250 ± 31	250 ± 31	0.91
Final BW, kg	288	52.6	300 ± 32	296 ± 32	296 ± 32	0.84
Mid-test metabolic BW, kg	64.9	9.54	67.0 ± 6.05	66.4 ± 6.07	66.7 ± 6.06	0.90
ADG, kg/d	0.67	0.17	0.68 ± 0.07	0.65 ± 0.07	0.67 ± 0.07	0.73
DMI, kg/d	6.1	0.95	6.5 ± 0.51	6.3 ± 0.51	6.2 ± 0.51	0.20
Feed conversion ratio, DMI : ADG kg	9.79	2.93	9.77 ± 1.15	10.67 ± 1.17	9.66 ± 1.16	0.24
Partial efficiency of growth	0.24	0.06	0.23 ± 0.02	0.22 ± 0.02	0.24 ± 0.02	0.41
Residual feed intake, kg/d	0.00	0.15	0.12 ± 0.02[d]	0.01 ± 0.02[e]	-0.13 ± 0.02[f]	<0.01
Weaning exit velocity, m/sec	2.50	1.35	2.58 ± 0.36	2.19 ± 0.37	2.54 ± 0.36	0.45
Weaning pen score	2.73	1.20	2.88 ± 0.22	2.36 ± 0.23	2.93 ± 0.22	0.11
Weaning temperament score	2.61	1.08	2.72 ± 0.25	2.28 ± 0.26	2.72 ± 0.25	0.17

[a]Data is pooled from Exp. I, II, and III. High = RFI was > 0.5 SD above the mean; Medium = RFI was ± 0.5 SD above and below the mean; Low = RFI was < 0.5 SD below the mean.

[b]Overall trait mean.

[c]Overall trait standard deviation.

[def]Least squares means within rows with different superscripts differ ($P \leq 0.01$).

an ADG of 0.67 kg/d (SD = 0.17; Table 2.3). Heifers on trial had an average DMI of 6.1 kg/d (SD = 0.95), a FCR of 9.79 DMI/kg of gain (SD = 2.93), PEG of 0.24 ADG/DMI for growth (SD = 0.06), and a RFI of 0.00 kg/d (SD = 0.15). Residual feed intake ranged from an efficient -0.63 kg/d to an inefficient 0.32 kg/d, resulting in a difference of 0.95 kg/d of DMI between the most and least efficient heifers. The average EV for heifers on trial was 2.50 m/sec (SD = 1.35), and PS was 2.73 (SD = 1.20), resulting in an average TS of 2.61 (SD = 1.08).

Differences in performance, feed efficiency traits, and temperament are presented in Table 2.3 and partial correlations between performance and feed efficiency traits are presented in Table 2.4. There were no differences in initial BW ($P = 0.91$), final BW ($P = 0.84$), $MBW^{0.75}$ ($P = 0.90$), or ADG ($P = 0.73$) among high, medium and low RFI heifers. There were also no differences in DMI ($P = 0.20$), FCR ($P = 0.24$), or PEG ($P = 0.41$) between these RFI efficiency groups. Residual feed intake efficiency groups were significantly different ($P < 0.01$). High RFI heifers had an average RFI of 0.12 ± 0.02 kg/d, medium heifers had a RFI of 0.01 ± 0.02 kg/d, and low heifers had a RFI of -0.13 ± 0.02 kg/d ($P < 0.01$). No differences were observed between RFI efficiency groups for EV ($P = 0.45$), PS ($P = 0.11$), or TS ($P = 0.17$).

Residual feed intake was not correlated ($P > 0.05$) with any traits measured in this study (Table 2.4). Dry matter intake was strongly correlated with initial (r = 0.96; $P < 0.01$) and final BW (r = 0.96; $P < 0.01$) as well as $MBW^{0.75}$ (r = 0.96; $P < 0.01$), and was moderately correlated to ADG (r = 0.44; $P < 0.01$) and PEG (r = -0.31; $P < 0.01$). However, DMI was not correlated to FCR ($P = 0.73$). Average daily gain had a strong

Table 2.4. Partial correlations of feed efficiency and performance traits in Brahman heifers

Trait[a]	Initial BW	Final BW	$MBW^{0.75}$	ADG	DMI	FCR	PEG	RFI
Initial BW	1.00	0.98[b]	0.99[b]	0.36[b]	0.96[b]	0.11	-0.35[b]	0.00
Final BW		1.00	0.99[b]	0.55[b]	0.96[b]	-0.08	-0.16	0.00
$MBW^{0.75}$			1.00	0.47[b]	0.96[b]	-0.01	-0.24[c]	0.00
ADG				1.00	0.44[b]	-0.78[b]	0.68[b]	0.00
DMI					1.00	0.03	-0.31[b]	0.16
FCR						1.00	-0.88[b]	0.04
PEG							1.00	-0.16
RFI								1.00

[a]In BW = shrunk initial BW, Out BW = shrunk final BW, $MBW^{0.75}$ = mid-test metabolic BW, FCR = feed conversion ratio, PEG = partial efficiency of gain, and RFI = residual feed intake.
[b]Correlations are different than zero ($P < 0.01$).
[c]Correlations are different than zero ($P < 0.05$).

correlation with PEG (r = 0.68; $P < 0.01$) and FCR (r = -0.78; $P < 0.01$), and was moderately correlated to initial BW (r = 0.36; $P < 0.01$), final BW (r = 0.55; $P < 0.01$), and $MBW^{0.75}$ (r = 0.47; $P < 0.01$). Partial efficiency of growth was moderately correlated to initial BW (r = -0.35; $P < 0.01$) and $MBW^{0.75}$ (r = -0.24; $P < 0.01$), and had a strong correlation with FCR (r = -0.88; $P < 0.01$). Partial efficiency of growth was not correlated to final BW ($P = 0.11$). Feed conversion ratio was not correlated with initial BW, final BW, or $MBW^{0.75}$ ($P > 0.05$). There was a very strong correlation between initial BW and final BW (r = 0.98; $P < 0.01$), initial BW and $MBW^{0.75}$ (r = 0.99; $P < 0.01$), and final BW and $MBW^{0.75}$ (r = 0.99; $P < 0.01$).

There were no correlations ($P > 0.05$) observed between any measures of temperament taken at weaning, and FCR, PEG, RFI, or ADG in the heifers used in this study (Table 2.5). Exit velocity was weakly correlated with initial BW (r = -0.25; $P = 0.01$), final BW (r = -0.23; $P = 0.02$), $MBW^{0.75}$ (r = -0.22; $P = 0.03$), and DMI (r = -0.27; $P = 0.01$). Pen score was not correlated ($P > 0.05$) to any measures of performance in this study, as well as DMI. Temperament score was not correlated with initial BW, final BW, or $MBW^{0.75}$, but was weakly correlated to DMI (r = -0.20; $P = 0.05$). There was a moderate correlation observed between PS and EV (r = 0.40; $P < 0.01$). Temperament score had a strong correlation with EV (r = 0.86) and PS (r = 0.81; $P < 0.01$).

There were no significant differences between the efficiency group for any digestive kinetics parameters measured or BW in Exp. I (Table 2.6), Exp. II (Table 2.7), or Exp. III (Table 2.8). Heifers in Exp. I evaluated for digestive kinetics had an average

Table 2. 5. Partial correlations between temperament measurements, performance traits, and measures of feed efficiency in growing Brahman heifers[a]

Trait[b]	EV	PS	TS
Initial BW	**-0.25**	0.03	-0.16
Final BW	**-0.23**	0.01	-0.16
$MBW^{0.75}$	**-0.22**	0.03	-0.14
ADG	-0.04	-0.04	-0.06
DMI	**-0.27**	-0.02	**-0.20**
FCR	-0.08	-0.04	-0.06
PEG	0.12	-0.04	0.05
RFI	0.06	0.09	0.07
EV	1.00	**0.40**	**0.86**
PS	-	1.00	**0.81**
TS	-	-	1.00

[a]Correlations in bold are different than zero at $P < 0.05$.

[a]In BW = shrunk initial BW, Out BW = shrunk final BW, $MBW^{0.75}$ = mid-test metabolic BW, FCR = feed conversion ratio, PEG = partial efficiency of gain, RFI = residual feed intake, EV= exit velocity, PS = pen score, TS = temperament score.

Table 2.6. Differences in digestive kinetics between high and low RFI Brahman heifers in Exp. I

Trait[a]	Mean[b]	SD[c]	RFI Group High	RFI Group Low	*P*-Value
Number Heifers			4	2	
BW	375	34.9	383 ± 18.0	357 ± 25.5	0.45
CM2, g DM/kg BW	19.8	8.2	20.9 ± 4.5	17.5 ± 6.4	0.68
MCRT, h	6.4	5.3	6.2 ± 3.0	6.8 ± 4.2	0.91
MCRTS, h	67.5	37.2	64.4 ± 20.6	73.6 ± 29.2	0.81
RTG, h	75.2	32.6	75.1 ± 18.2	75.5 ± 25.8	0.99
TAU, h	7.8	10.8	10.7 ± 5.5	1.9 ± 7.7	0.41
FO, g DM/kg BW	9.1	453	10.4 ± 2.27	6.5 ± 3.2	0.38

[a]CM2 = age-independent compartment turnover, MCRT = age-dependent residence time, MCRTS = age-dependent age-independent residence time, RTG = gastrointestinal residence time, TAU = first appearance of marker, FO = Fecal output.

Table 2.7. Differences in digestive kinetics between high and low RFI Brahman heifers in Exp. II

Trait[a]	Mean[b]	SD[c]	RFI Group High	RFI Group Low	*P*-Value
Number Heifers			5	3	
BW	305	35.0	290 ± 13.9	329 ± 18.0	0.14
CM2, g DM/kg BW	14.0	3.7	15.0 ± 1.6	12.3 ± 2.1	0.35
MCRT, h	7.0	3.1	6.0 ± 1.3	8.6 ± 1.7	0.29
MCRTS, h	42.4	19.2	48.2 ± 8.5	33.1 ± 10.9	0.32
RTG, h	49.6	21.4	54.8 ± 9.7	40.9 ± 12.5	0.41
TAU, h	7.0	5.0	6.6 ± 2.4	7.8 ± 3.1	0.77
FO, g DM/kg BW	10.5	2.7	9.5 ± 1.1	12.0 ± 1.5	0.23

[a]CM2 = age-independent compartment turnover, MCRT = age-dependent residence time, MCRTS = age-dependent age-independent residence time, RTG = gastrointestinal residence time, TAU = first appearance of marker, FO = Fecal output.

Table 2.8. Differences in digestive kinetics between high and low RFI Brahman heifers in Exp. III

Trait[a]	Mean[b]	SD[c]	RFI Group High	RFI Group Low	*P*-Value
Number Heifers			5	3	
BW	255	22.7	267 ± 16.2	245 ± 13.3	0.41
CM2, g DM/kg BW	8.0	2.3	9.3 ± 1.4	9.1 ± 1.1	0.21
MCRT, h	4.1	4.1	3.8 ± 3.4	4.3 ± 2.7	0.92
MCRTS, h	28.8	9.7	22.1 ± 6.1	33.3 ± 5.0	0.25
RTG, h	43.2	13.0	33.7 ± 7.9	49.5 ± 6.5	0.22
TAU, h	14.4	13.2	11.7 ± 10.6	16.2 ± 8.6	0.76
FO, g DM/kg BW	8.7	3.8	9.8 ± 3.0	7.9 ± 2.4	0.66

[a]CM2 = age-independent compartment turnover, MCRT = age-dependent residence time, MCRTS = age-dependent age-independent residence time, RTG = gastrointestinal residence time, TAU = first appearance of marker, FO = Fecal output.

BW of 375 kg (SD = 35), an average CM2 of 19.8 g DM/kg BW (SD = 8.2), MCRT of 6.4 h (SD = 5.3), MCRTS of 67.5 h (SD = 37.2), RTG of 75.2 h (SD = 32.6), TAU of 7.8 h (SD = 10.8), and FO of 9.1 g DM/kg BW (SD = 4.5). Heifers in Exp. II evaluated for digestive kinetics had an average BW of 305 kg (SD = 35), CM2 of 14.0 g DM/kg 21.4), TAU of 7.0 h (SD = 5.0), and a FO of 10.5 g DM/kg BW (SD = 2.7). Heifers in Exp. III evaluated for digestive kinetics had an average BW of 255 kg (SD = 23), CM2 of 8.0 g DM/kg BW, MCRT of 4.1 h (SD = 4.1), MCRTS of 28.8 h (SD = 9.7), RTG of 43.2 h (SD = 13.0), TAU of 14.4 h (SD = 13.2), and a FO of 8.7 g DM/kg BW (SD = 3.8).

Summary statistics for heifers evaluated for fecal VFA concentration are presented in Table 2.9. Fecal VFA concentrations were not significantly different between the RFI efficiency groups (Table 2.10). The overall mean acetic acid concentration was 7.77 mM (SD = 1.37), proprionic acid concentration was 1.46 mM (SD = 0.41), isobutyric acid concentration was 0.13 mM (SD = 0.04), butyric acid concentration was 0.53 mM (SD = 0.18), isovaleric concentration was 0.09 mM (SD = 0.03), and valeric acid concentration was 0.11 mM (SD = 0.03).

The methods used to determine apparent DMD in this study were not sensitive enough to account for the weekly variation associated with ADIA. Therefore caution should be used when trying to interpret the results reported. There were no differences in apparent DMD observed among the RFI efficiency groups (P = 0.61). Average DMD was 497.6 ± 41.7 g/kg DM for Exp. I and 571.6 ± 35.3 g/kg DM for Exp. II for all heifers. Overall DMD for both trials was 544.1 ± 52.0 g/kg DM for all heifers. Within

Table 2.9. Summary statistics of fecal VFA concentration measured in three experimental trials in growing Brahman heifers[a]

Trait	Exp. I	Exp. II	Exp. III
Number of heifers	23	12	13
Age, mo	17.4 ± 0.64	12.0 ± 0.82	7.0 ± 0.64
Residual feed intake, kg/d	0.00 ± 0.31	0.01 ± 0.04	-0.01 ± 0.08
Acetic acid, mM	7.71 ± 1.32	7.99 ± 0.84	7.69 ± 1.86
Proprionic acid, mM	1.54 ± 0.45	1.33 ± 0.33	1.47 ± 0.38
Isobutyric acid, mM	0.12 ± 0.03	0.11 ± 0.03	0.15 ± 0.05
Butyric acid, mM	0.49 ± 0.09	0.49 ± 0.16	0.63 ± 0/27
Isovaleric acid, mM	0.07 ± 0.02	0.08 ± 0.03	0.11 ± 0.04
Valeric acid, mM	0.10 ± 0.02	0.10 ± 0.03	0.12 ± 0.04

[a]Data is reported as mean ± SD.

Table 2.10. Difference in fecal VFA concentration for Brahman heifers evaluated for RFI

			RFI group[a]			
Trait	Mean[b]	SD[c]	High	Medium	Low	*P*-Value
Number of Heifers			21	10	17	
Residual feed intake, kg/d	0.00	0.14	0.07 ± 0.03[d]	0.02 ± 0.04[d]	-0.10 ± 0.04[e]	< 0.01
Acetic acid, mM	7.77	1.37	7.96 ± 0.30	7.83 ± 0.44	7.51 ± 0.34	0.61
Proprionic acid, mM	1.46	0.41	1.54 ± 0.09	1.43 ± 0.13	1.44 ± 0.10	0.85
Isobutyric acid, mM	0.13	0.04	0.13 ± 0.01	0.12 ± 0.02	0.13 ± 0.01	0.63
Butyric acid, mM	0.53	0.18	0.53 ± 0.05	0.58 ± 0.07	0.51 ± 0.06	0.69
Isovaleric acid, mM	0.09	0.03	0.09 ± 0.01	0.08 ±0.01	0.09 ± 0.01	0.61
Valeric acid, mM	0.11	0.03	0.11 ± 0.01	0.11 ± 0.01	0.11 ± 0.01	0.97

[a]Data are pooled from Exp. I, II, and III. High = RFI was > 0.5 SD above the mean; Medium = RFI was ± 0.5 SD above and below the mean; Low = RFI was < 0.5 SD below the mean.

[b]Overall trait mean.

[c]Overall trait standard deviation.

[de]Least squares means within rows with different superscripts differ ($P \leq 0.01$).

animal CV for DMD determined in Exp. I averaged 23.86%, with values ranging from 11.51-to-40.72% DM. In Exp. II, within animal CV for DMD averaged 18.36%, and ranged from 6.23-to-33.80%. The overall average within animal CV for DMD for both experiments was 20.40%. The CV of DMD between animals was 8.38% for Exp. I, and combined was 9.55%. Data can be found in Appendix A.

Discussion

As expected, Brahman heifers with a low RFI did not differ from medium or high RFI heifers in initial BW, final BW, $MBW^{0.75}$, or ADG, as RFI has been shown to be independent of these performance traits in *Bos taurus* type (Arthur et al., 2001b; Hennessy and Arthur, 2004; Nkrumah et al., 2004) and Santa Gertrudis cattle (Brown, 2005). These findings indicate that selection for increased efficiency based on RFI in *Bos indicus* cattle should not have an influence on mature BW.

Feed conversion ratio, although independent of BW in this trial, had a strong negative correlation with ADG. This indicates that selection based on FCR would result in an increase in the rate of gain, potentially increasing mature BW over time. Nkrumah et al. (2004), Arthur et al. (2001a,b), and Hennessy and Arthur (2004) also observed a similar relationship between FCR and ADG in *Bos taurus* type cattle as well as Brown (2005) using *Bos taurus* crossbred and Santa Gertrudis cattle. Hennessy and Arthur (2004) found FCR to be moderately correlated with initial and final BW (r = 0.49 and 0.29, respectively) in Hereford cattle, while Nkrumah et al. (2004) using *Bos taurus* crossbred cattle, and Brown (2005) using *Bos taurus* crossbred and Santa Gertrudis cattle found no correlations between FCR and measures of BW over the feeding period.

Partial efficiency of growth had a strong positive correlation with ADG, and a moderate correlation with initial BW and $MBW^{0.75}$ in the Brahman heifers utilized in this study. These findings indicate that selection for increased efficiency could potentially increase mature BW. Nkrumah et al. (2004) reported, although not as strong, a positive correlation ($r = 0.24$ and 0.29) between PEG and ADG in *Bos taurus* crossbred and Santa Gertrudis cattle, but found no correlation with BW measurements. Arthur et al. (2001b) reported that PEG was slightly negatively correlated to ADG ($r = -0.14$) and BW ($r = -0.08$) in Charolais cattle. Hennessy and Arthur (2004) found no correlation between PEG and ADG in Hereford cattle, but did report that PEG had a moderately negative correlation to BW ($r = -0.40$). The variation in correlations reported in the literature may be a result of the variation in formulas used to calculate maintenance feed requirements, and the accuracy of those measurements with the different types of cattle utilized in the different studies.

There were no significant differences in DMI between the RFI efficiency groups in this study. Many other researchers have found significant differences and strong correlations between RFI and DMI (Arthur, et al., 1996; Arthur et al., 2001a; Hennessy and Arthur, 2004; Nkrumah, et al., 2004). In this study, because the heifers were limit fed, based on a proportion of their BW, variation in DMI is a product of the variation in BW and feed refusals. As would be expected with this type of feeding strategy, DMI was strongly correlated to all BW measurements. Therefore, because RFI is independent of growth performance traits, DMI (with minimal feed refusals) should not be correlated with RFI, as seen in this study. More importantly, relative to their level of production, efficient heifers based on RFI consumed less than would be expected for that level of production. Therefore, low RFI animals produce greater output for the level of input, than their inefficient counterparts. This makes the residual a more relevant measure of efficiency than actual DMI. Partial efficiency of growth in Brahman heifers was slightly less correlated to DMI than what has been reported by: Arthur et al. (2001b; r = -0.69) in Angus cattle, Nkrumah, et al. (2004; r = -0.52) in *Bos taurus* crossbred cattle, Hennessy and Arthur (2004; r = -0.67) in Hereford cattle; and Brown (2005; r = -0.50; $P < 0.05$) in *Bos taurus* crossbred and Santa Gertrudis cattle, although still indicating that selection for increased efficiency based on PEG should reduce DMI over time. Similar to the reports of Hennessy and Arthur (2004) and Brown (2005), the correlation between FCR and DMI was not different from zero. This infers that selection for efficiency, based on FCR, should not have an effect on DMI. Other studies have reported more moderate correlations between these two measurements: Arthur et al. (2001a,b; r = 0.23 and r = 0.48) and Nkrumah, et al. (2004; r = 0.49). These findings, along with previous reports, indicate greater merit in the utilization of PEG as a measure of efficiency over FCR because of its decreased association with ADG and the influence it has on reducing DMI.

Residual feed intake was not correlated with FCR or PEG in this study, but PEG had a strong negative correlation with FCR. This suggests that selection for efficiency based on RFI would have no effect on FCR or PEG over time in Brahman heifers. Many studies utilizing *Bos taurus* type breeds of cattle, have shown that RFI is correlated with PEG and FCR indicating that selection for increased efficiency in RFI would also increase efficiency based on FCR and PEG (Arthur, et al., 1996; Arthur et al., 2001b; Hennessy and Arthur, 2004; Nkrumah, et al., 2004). Brown (2005) reports results utilizing *Bos taurus* crossbred and *Bos indicus* influenced (Santa Gertrudis) cattle that agree with the finding reported in *Bos taurus* breeds. These same authors have observed similar correlations to those reported in this study between PEG and FCR, inferring selection for increased efficiency in one measurement should increase efficiency in the other measurement. The lack of association between RFI and PEG or FCR in this study may be explained by the feeding strategy which limits the variation in DMI to variation in BW. Partial efficiency of growth and FCR were more strongly associated with ADG in Brahman heifers compared to the *Bos taurus* breeds used in other studies. In the current study, ADG was moderately correlated to all BW measurements. The correlation between FCR and PEG seems to be a product of their strong relationship with ADG, as RFI is independent of ADG.

Animal temperament has a negative impact on numerous aspects of beef cattle production such as: BW gain (Voisinet et al., 1997b), milk production (Breuer et al., 2000), carcass tenderness, and the occurrences of dark-cutters (Voisinet et al., 1997a). Temperamental cattle are those that easily become excited and agitated when handled in a confined area or a stressful situation such as a squeeze chute or a crowding pen (Voisinet et al., 1997a; Voisinet et al., 1997b). Archer et al. (1997) determined that a 70-d feeding trial was required to minimize variation in ADG, and 35-d was required for DMI. The length of test time required for feed efficiency measurements makes them economically unfeasible in most production settings. Weaning is an ideal time for produces to take measurements that may be used as an indicator of efficiency because the animals are already being handled. Curley et al. (2006) reported a reduction in EV in Brahman bulls over time, but saw no change in rank indicating that temperamental cattle stay temperamental and calm cattle remain calm.

Our results are similar to Brown (2005) who reported that neither subjective nor objective measures of temperament were associated with PEG, FCR, RFI, or ADG. Feeding strategies utilized in this experiment may have contributed to the lack of difference in ADG between calm and temperamental cattle. Richardson et al. (2000) found no difference in EV, an objective measure, between steers divergently selected for RFI at four different points during their feeding trial. Burrow and Dillion (1997) and Voisinet et al. (1997b) found that calmer animals with a lower EV had a greater ADG than wilder. Exit velocity had a weak negative correlation ($P = 0.02$) with all measures of BW indicating that the heavier animals were less excitable. There was also a weak negative correlation ($P = 0.01$) between EV and DMI due to the feeding strategies implemented in this study. Pen score, a subjective measure, was not associated with any BW measurements taken ($P = 0.87$), and consequently it was not associated with DMI ($P = 0.75$). Due to the lack of association between PS and these performance traits, correlations between TS, a combination of subjective and objective measurements, and BW measurements were not different from zero ($P > 0.11$). Temperament score, although weaker than EV, did have a weak negative correlation with DMI ($r = -0.20$; $P = 0.05$). Again, in this study, this correlation is more a product of BW than a product of DMI. These findings, similar to those of Richardson et al. (2000) and Brown (2005), suggest that temperament measurements are not a valid means of predicting feed efficiency traits. However, although not related to ADG in this study, EV taken at weaning may have some merit in its use for prediction of BW. Exit velocity taken at weaning was moderately correlated ($P < 0.01$) with PS taken at weaning. Curley et al. (2006) also found a moderate correlation with EV and PS in the first of three temperament evaluations in Brahman bulls.

Accuracy of determining digestive kinetics in ruminants relies predominantly on the placement of a digestive marker with a meal consumed by the animal, and the collection of enough fecal samples to accurately model the fecal Yb concentration. Heifers must consume enough of the Yb dose in a short period of time to achieve the pulse affect of the marker, creating a peak in fecal Yb concentration. There were no significant differences in any digestive dynamics parameters determined in theses experiments. One potential reason for the lack of variation between the efficiency groups is the large SE for the digestive kinetic parameters. Passage rate for these heifers were much faster than what were expected. As a result, the peak of fecal Yb concentration also occurred much sooner than expected. Initial fecal samples for those heifers with a very fast rate of passage were taken during or directly following the peak of the fecal Yb concentration making it difficult to accurately modeling the fecal Yb concentration.

The diet of a ruminant requires it to have a specialized digestive system that is capable of turning feedstuffs consumed into energy. This is achieved through flow through a segmented digestive system that allows for microbial and enzymatic digestion. Primary microbial digestion occurs in the reticulo-rumen, and secondary microbial digestion occurs in the cecum and large intestines. Enzymatic digestion occurs in the abomasum and small intestines (Merchen et al., 1997). Site of digestion determines the type of digestion that ingested materials undergo, which influences the products produced. Starch digestion in the small intestines provides more value than starch digested in the rumen (Owens et al., 1986). Microbial fermentation in the large intestines produces VFA, CH_4, H_2, and CO_2 (Hoover, 1978; Wolin, 1981). The quantity of fermentable substrates that are able to by-pass the rumen and small intestines regulate the extent of fermentation in the large intestines (Hoover, 1978). There were no differences in fecal VFA concentration between high and low RFI heifers, indicating that there was no difference in the amount of fermentable substrate that reached the large intestines between the efficiency groups.

Brown (2005), using acid insoluble ash as an internal marker, reported that DMD had a negative correlation ($r = -0.32$; $P < 0.05$) with RFI. Efficient animals tended ($P < 0.13$) to have a 6.6 % greater DMD than inefficient animals. Richardson et al. (1996), using natural alkanes, investigated the variation in DMD in British heifers and bulls during the RFI evaluation period. Although not significant, low RFI animals had a tendency to digest their feed 1% better than the high RFI animals. These authors show that this small difference equates into a 2.3% decrease in daily feed required for a 450 kg calf gaining at 1.3 kg/d with a diet representative of their study (69% DMD). Richardson et al. (2004) following one generation of divergent selection for RFI in Angus cattle found a negative correlation ($r = -0.44$, $P < 0.05$) between DMD and RFI in these animals, using total fecal collection to determine apparent DMD, during an animal housing period while accessing metabolic processes. These reports indicate the potential for variation in DMD to explain some of the subsequent variation in RFI. The sample collection procedures utilized in the current trial revealed an extremely large amount of variation in DMD from week to week within an individual animal. Average DMD taken over the 10 wk period are not unrealistic, and produce a much smaller CV. However, the problem with accepting these results lies in the large amount of variation in the values used to produce these averages. There are a number of potential reasons for the variation in DMD from week to week for individual animals. Fecal samples were collected from the rectum of individual animals prior to feeding (~24 h following the previous feeding). The ration utilized for these experiments contained a relatively small amount of ADIA. Variation in feeding patterns between animals may have resulted in a variation in ADIA excretion. Location of the fecal samples collected, whether they were taken from an observed defecation, near the rectum, or further down the tract via palpation could also provide a potential source of variation. Temperamental responses by the cattle when they were being moved from their pens to the working facilities potentially could cause a change in fecal characteristics and alter gut function. These results show that in these experiments, excretion of ADIA was far too variable to be collected once weekly with any kind of accuracy.

Conclusion

The results of this study indicate that through selection based on RFI, producers can select for efficient animals without influencing rate of gain or BW measurements. These results also indicate that *Bos indicus* cattle appear to have efficiency traits similar to either *Bos taurus* or *Bos indicus* influenced breeds of cattle. Therefore utilization of RFI as a measure of feed efficiency should be as equally valid in *Bos indicus* cattle as it is in *Bos taurus* cattle. The major drawback to the use of other measures of efficiency is that selection for increased efficiency results in an increased rate of gain, as seen with FCR and PEG in this study. An increase in the rate of gain over a period of time potentially could increase mature BW. As seen in other studies, RFI was independent of ADG and all BW measurements. As a result of the feeding strategy and the lack of association between RFI and BW measurements, DMI was not significantly different between the efficiency groups. This shows that even when intake is limited, RFI is not associated with BW. However, low RFI heifers consumed less feed than predicted for their given level of production, compared to their inefficient counterparts. Although PEG and FCR have the potential to increase mature BW as a result of an increase in ADG, PEG shows to have a greater potential to decrease DMI than FCR, through selection. Temperament measurements taken at weaning were not related to any measures of feed efficiency in this study. Digestive kinetics, site of digestion, and apparent DMD did not appear to be different between the efficiency groups. There is sufficient enough evidence in the literature to warrant further investigation into the relationship between RFI and DMD.

CHAPTER III

SOURCES OF VARIATION IN RESIDUAL FEED INTAKE (RFI) ON PASTURE AND HOW THEY RELATE TO RFI DETERMINED IN CONFINEMENT

Introduction

Providing feed and forage to beef cattle represents a large portion of the cost associated with production. Residual feed intake is one of many measures of feed efficiency utilized in beef cattle. This measure of efficiency identifies animals that eat less than expected for their given level of production. Efficiency is determined by the residual between actual and expected feed intake. Animals with a low residual or low RFI are considered to be more efficient because they consumed less feed than would be expected for their level of production, while animals with a high residual or high RFI are considered to be less efficient because they consume more feed than would be expected for their level of production. Residual feed intake is an attractive measure of feed efficiency because it is independent of the production traits used to calculate it, meaning that selection for efficiency based on RFI should not affect rate of gain or mature BW (Arthur et al., 2001b; Hennessy and Arthur, 2004; Nkrumah et al., 2004; Brown, 2005).

In order to be a beneficial tool for production, the relationship between RFI determined in confinement in young growing animals, and the performance by those animals on pasture must be determined. Grazing is the primary means of nutrient intake for cattle on forage (Lippke, 2002). Variation in activity and feeding behavior has been noted between efficient and inefficient animals. Differences in feeding behavior in swine

(Van Felde et al., 1996), and activity level in poultry (Luiting et al., 1994) have helped explain the variation in RFI in those species. Similar differences in feeding behavior have been seen in cattle evaluated for RFI in confinement feeding (Richardson et al., 2000). Few studies have evaluated the relationship between RFI determined in confinement and RFI on pasture. Herd et al. (1998) found no difference in intake for mature cows grazing on pasture, evaluated for RFI post weaning, but did indicate a potential for a correlation between post weaning RFI measurements and forage intake on pasture. Archer et al. (2002) found strong genetic correlations with intake related traits in confinement feeding, measured shortly after weaning, and then measured again as mature cows. Therefore, the objective of this study was to evaluate grazing behavior and forage intake on pasture in Brahman heifers previously evaluated for RFI in confinement feeding.

Materials and Methods

Twelve Brahman heifers (21-to-24 mo of age), previously evaluated for RFI in confinement, were used to determine sources of variation in RFI on pasture. Heifers were evaluated for RFI in a 70 d feeding trial (Exp. 1: fall 2004) in a Calan gate system at the TAES, Overton (Chapter II). Heifers were fed a 12% crude protein receiving ration (Table 2.1) at a rate of 2.2% of their BW daily. Heifers were weighed weekly, and feed allocations were adjusted to reflect their weight. Residual feed intake was determined by the residual between actual DMI and expected DMI for their level of production. Expected DMI was determined by linear regression of actual DMI, ADG, and mid-test $BW^{0.75}$. Six high RFI and six low RFI heifers were transported to TAES, Uvalde, to be evaluated for grazing behavior and forage intake following the RFI evaluation. Heifers grazed irrigated Fescue and Ryegrass from the middle of February to May 2006.

Grazing Behavioral Determination. Randomly throughout the grazing trial, four animals (two high RFI and two low RFI) were fitted with the Graze IGER behavior recorders (Institute of Grassland and Environmental Research, North Wyke, Okehampton, Devon EX20 2SB UK) to access their grazing behavior by recorded observations of jaw movements. Recorders were placed on the animals around 1200 and animals were allowed to graze for 24 h while grazing data were recorded. Following each 24 h observation period the halters were removed and data flash-cards that contained the grazing data were removed and replaced with a new flash card. Halters were put back on the same heifers for a second 24 h observation period. Data from the flash-cards were downloaded to a computer and analyzed with the Graze software (version 0.80; Institute of Grassland and Environmental Research, North Wyke, Okehampton, Devon EX20 2SB UK). Following a complete 48 h observation period, halters were removed from animals and batteries were allowed to charge overnight. Flash cards were also removed and handled as stated above. The following day (after charging) the protocol was repeated with new animals. All animals were evaluated four times over the entire observation period. The Graze software was used to differentiate between grazing time, ruminating time, bites, chews, and idle time (any activity other than grazing or ruminating). Each heifers individual 24 h observation period was divided into a 6-h morning (AM, 0530-to-1130) and a 6-h afternoon (PM, 1430-to-2030) activity periods.

Forage Intake and Apparent Digestibility Determination. Following a 30 d adjustment period, heifers were dosed with synthetic alkanes by placing a Captec Alkane Controlled Release Capsule (CRC; Nufarm Health and Science, Auckland, New Zealand) into the rumen. The CRC is designed to release 400 mg/d of C32 alkane for approximately 20 d. Ten days after dosing, individual fecal samples were collected daily for 7 d by palpation of the rectum of each animal around 1200 to coincide with grazing behavior data collection. A minimum of 100 forage grab samples representative of the entire paddock were collected every morning prior to fecal sampling to determine alkane concentrations in the forage consumed. Forage and fecal samples were freeze-dried and ground to pass a 1-mm screen. Alkanes and C_{34}, an internal standard, were extracted and then quantified using gas chromatography as described by Mayes et al. (1986). One high RFI heifer continually regurgitated the alkane CRC, so she was not evaluated for forage intake. Apparent DMD was determined by predicting fecal output by using the ratio forage alkane concentration to fecal alkane concentration (Dove and Mays, 1991).

Statistical Analysis. To determine variation in grazing behavior for the morning and afternoon activity periods, individual animal’s mean grazing, ruminating, and idle time as well as the number of bites per minute taken were calculated using each complete observation period. Differences in the mean activities between the high and low RFI animals, as well as RFI, and BW were determined by using the PROC GLM procedures of SAS (SAS Inst. Inc., Cary, North Carolina). Least Squares Means were used for mean separation between high and low RFI groups. The model included RFI as the class variable, and each animal's individual mean time for grazing, ruminating, bites per minute, idle times, BW, and residual as the dependent variables.

Forage intakes were estimated using long chain alkanes as an internal marker. Estimated DMI was then divided by BW, taken on d 70 of RFI evaluation, to determine DMI as a portion of BW. The difference in estimated forage intake, as a portion of BW, between high and low RFI heifers was determined by the least squares procedures of SAS. PROC MIXED was used to examine the effect RFI had on estimated forage intake for both C31:C32 and C33:C32 alkane pairs. Repeated measures of PROC MIXED were performed for a factorial analysis of time and RFI effects on forage intake estimated by C31:32 and C33:32 alkane pairs throughout the duration of sample collection. An unstructured covariance model was used for this analysis. Variation in apparent digestibility between the efficiency groups was determined by PROC GLM of SAS. The model included RFI as the class variable, and apparent DMD as the dependent variables.

Results

Differences in RFI, BW, and grazing activities are presented in Table 3.1. Heifers evaluated for grazing behavior had a mean RFI of -0.02 (SD = 0.7), determined in confinement feed efficiency evaluation. During the 70-d confinement feed efficiency evaluation period, low RFI heifers consumed less ($P < 0.01$) than expected for their given level of production than high RFI heifers. Final BW taken at the end of the RFI observation period, prior to heifers being put on pasture, were not different among the efficiency groups ($P = 0.66$). Average BW for all heifers was 360 ± 20 kg. No

Table 3.1. Characterization of activities associated with grazing behavior during both the morning and afternoon grazing period in high and low residual feed intake Brahman heifers[a]

			RFI Group		
Activity[b]	Mean[c]	SD[d]	High	Low	*P*-value
Number of heifers	-	-	6	6	-
Residual feed intake, kg/day	-0.02	0.7	0.53 ± 0.1	-0.57 ± 0.1	< 0.01
BW, kg	360	20	359 ± 3	361 ± 3	0.66
AM grazing time, min	91.1	26.5	91.3 ± 11.4	91.0 ± 11.4	0.99
AM ruminating time, min	88.4	21.1	80.7 ± 8.4	96.1 ± 8.4	0.22
AM idle time, min	180.4	30.9	186.9 ± 12.9	173.9 ± 12.9	0.49
AM bites/min	29.5	5.6	28.3 ± 2.3	30.7 ± 2.3	0.48
PM grazing time, min	172.1	16.3	169.3 ± 6.8	174.9 ± 6.8	0.57
PM ruminating time, min	88.9	16.4	92.0 ± 6.9	86.0 ± 6.9	0.55
PM idle time, min	101.0	15.2	102.3 ± 6.5	99.7 ± 6.5	0.66
PM Bites/min	35.1	6.6	36.3 ± 2.8	33.8 ± 2.8	0.53

[a]Both morning (0530-to-1130) and afternoon (1430-to-2030) activity observation periods were 360 min each.
[b]BW = final BW taken during RFI evaluation prior to grazing evaluation, Idle time = any activity other than grazing or ruminating, bites/min = total number of bites of forage taken / total grazing time.
[c]Overall trait mean.
[d]Overall trait standard deviation.

significant differences were observed between high and low RFI heifers in any measure of grazing activity for either morning or afternoon activity periods. Mean grazing time for the AM observation period was 91.1 min (SD = 26.5) accounting for 25.3% of the observation period and 172.1 min (SD = 16.3) for the PM observation period accounting for 47.8% of the observation period. Mean ruminating time for the morning observation period was 88.4 min (SD = 21.1) accounting for 24.6% of the observation period, and afternoon ruminating time was 88.9 min (SD = 16.4) accounting for 24.7% of the afternoon observation period. Mean idle time was 180.4 min (SD = 30.9) accounting for 50.1% of the morning observation period, and 101.0 min (SD = 15.2), accounting for 28.1% of the afternoon observation periods. Heifers took 29.5 bites/min (SD = 5.6) in the morning, and 35.1 bites/min (SD = 6.6) in the afternoon observation period

Natural odd chain alkanes were used as an internal marker along with dosed even chained alkanes to quantify forage intake on pasture. Variation in forage alkane concentrations are presented in Figure 3.1, as well as daily intake between high and low RFI heifers determined by C31:C32 alkanes and intakes determined by C33:32 are presented in Figure 3.2. Forage samples contained more C31 alkanes (0.3778 mg/kg DM) than C33 alkanes (0.0988 mg/kg DM). No C32 alkanes were recovered in any forage sample collected. Average intake for the 7-d sampling period determined by C31:C32 alkanes were 7.55 kg/d (SD = 0.42) for all heifers and 9.04 kg/d (SD = 0.50) for intake determined by C33:C32 alkanes. Intakes ranged from 5.53-to-10.19 kg/d determined by C31:C32 alkanes and 6.84-to-13.34 kg/d determined by C32:C33 alkanes for all heifers. Estimated intakes as a proportion of BW (kg/100 kg of BW) over the 7-d

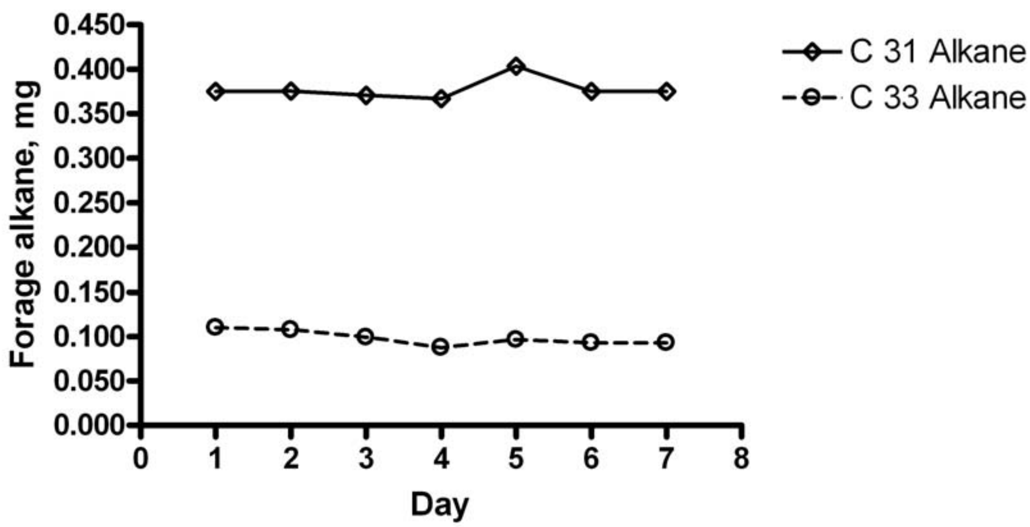

Figure 3.1. Forage alkane concentration for both C31 and C33 alkanes over the 7-d sampling period.

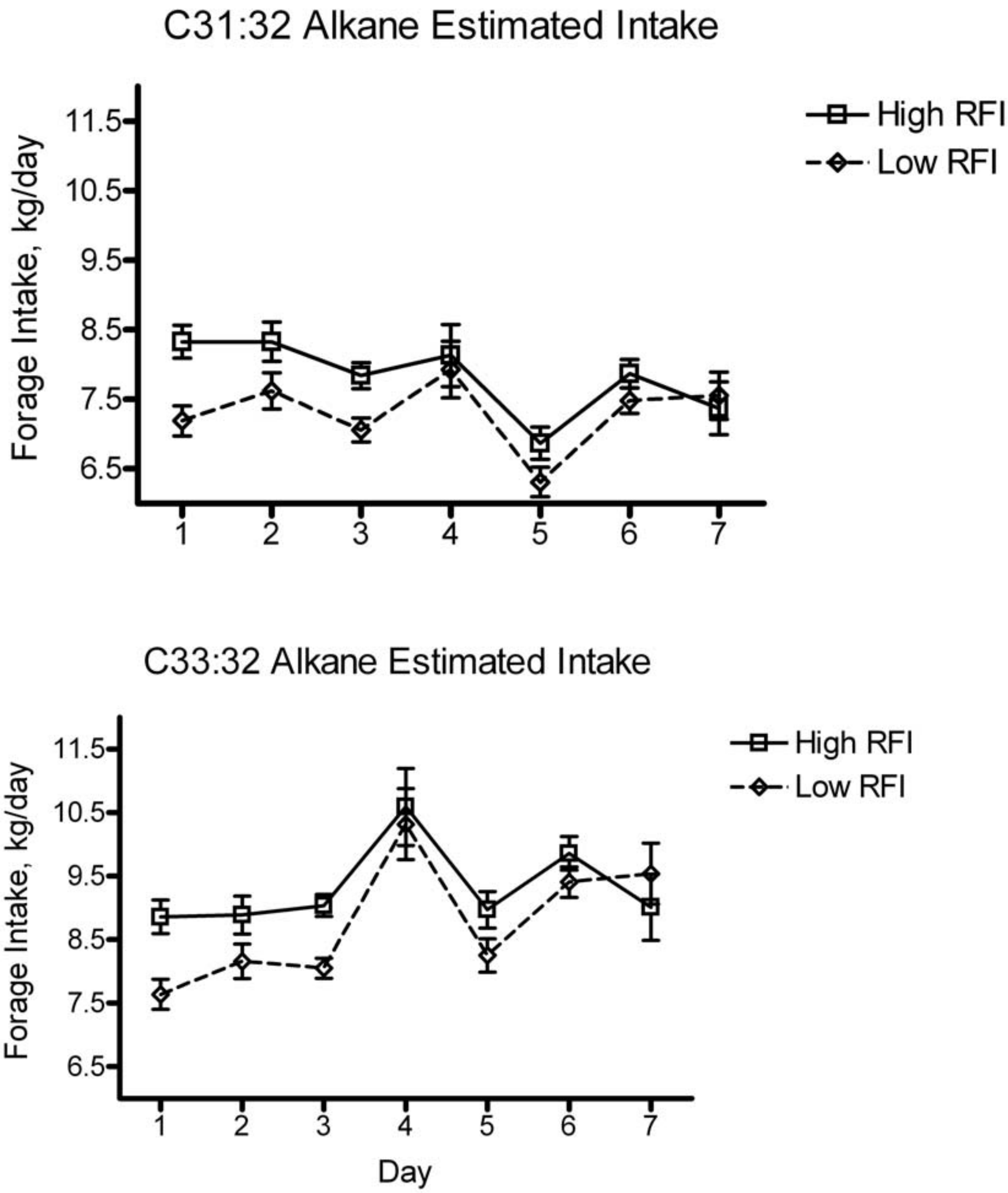

Figure 3.2. Forage intake estimations for high and low RFI Brahman heifers for both C 31:32 and C 33:32 alkane pairs over the 7-d sampling period.

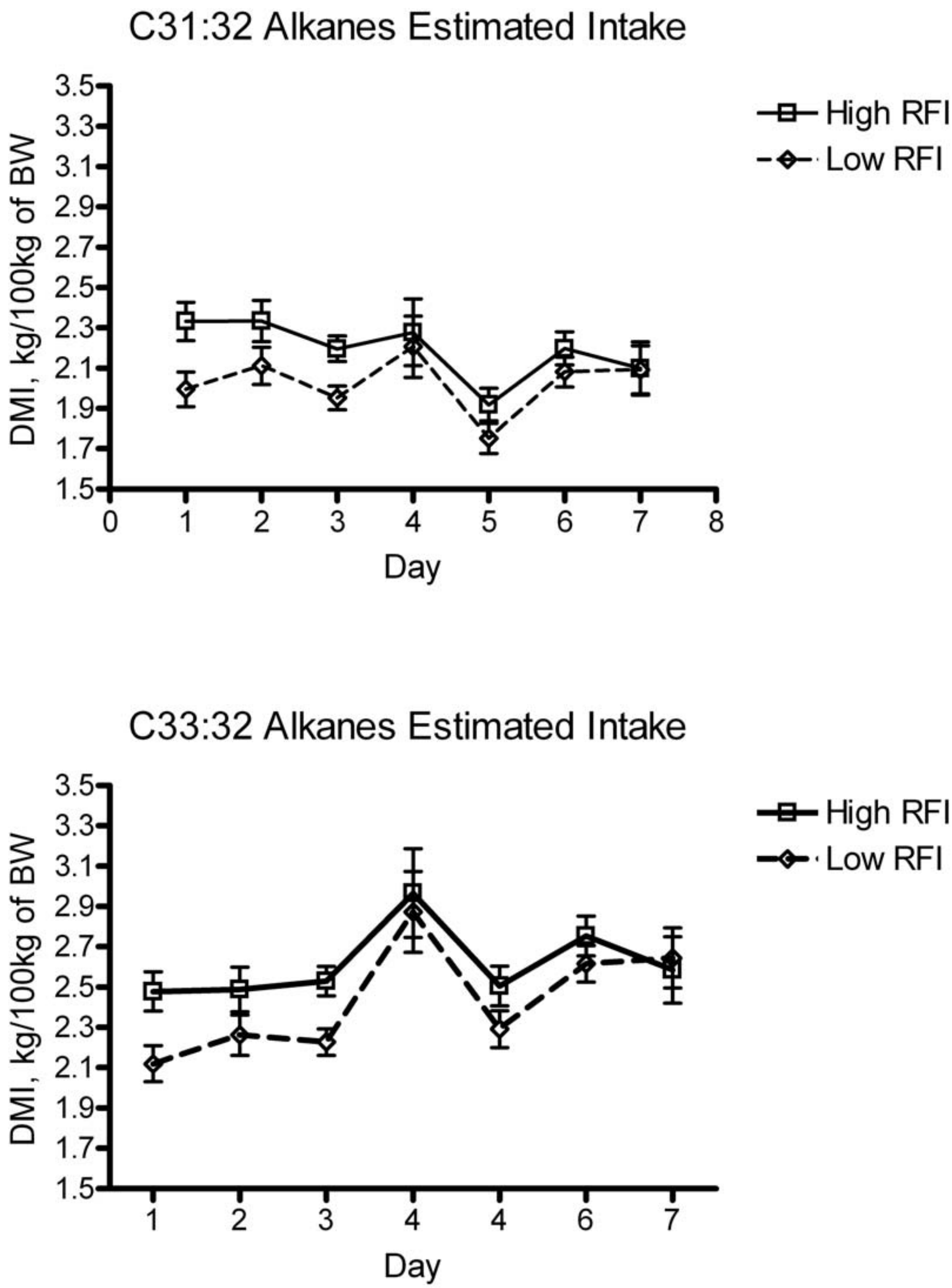

Figure 3.3. Forage intake estimations as a proportion of BW for high and low RFI Brahman heifers for both C 31:32 and C 33:32 alkane pairs over the 7-d sampling period.

sampling period are presented in Figure 3.3. Intakes as a proportion of BW were not different between the efficiency groups determined by C31:32 alkane pairs (*P* = 0.15) or C33:32 alkane pairs (*P* = 0.19). Heifers averaged 2.11 (SD = 0.27) kg/100 kg of BW for intakes estimated by C31:32 alkane pairs, and 2.52 (SD = 0.36) kg of DMI/100 kg of BW for intakes estimated by C33:32 alkane pairs. Intakes ranged from 1.46-to-3.06 kg/100 kg BW determined by C31:C32 alkanes and 1.93-to-4.01 kg/100 kg BW determined by C32:C33 alkanes for all heifers. Day had a significant influence on intake as a proportion of BW for both C31:32 alkane pairs (*P* = 0.01) and C33:32 alkane pairs (*P* = 0.01). There was no RFI*Day interaction for intake as a proportion of BW determined by C31:32 alkane pairs (*P* = 0.17), but there was a RFI*Day interaction determined by C33:32 alkane pairs (*P* = 0.02).

Natural odd-chain alkanes were used to determine apparent DMD between the RFI efficiency groups (Table 3.2). There were no differences between the efficiency groups in apparent DMD determined by either C31 (*P* = 0.62) or C33 (*P* = 0.73) alkanes. Overall heifers had an average apparent DMD determined by C31 alkanes of 759.5 g/kg DM (SD = 4.6), and an apparent DMD determined by C33 alkanes of 798.7 g/kg DM.

Discussion

It is important to understand how RFI determined in confinement relates to performance on pasture. It is important to note that the Graze IGER behavior recorders are extremely sensitive machines taking sensitive measurements. When an instrument this sensitive is placed on animals of this size, occasional equipment malfunction is

Table 3.2. Differences in apparent DMD between high and low RFI Brahman heifers on pasture

	Mean	SD	RFI Group[a] High	RFI Group[a] Low	*P*-value
Apparent DMD C31 alkanes, g/kg DM	759.8	4.7	760.6 ± 2.1	759.1 ± 1.9	0.62
Apparent DMD C33 alkanes, g/kg DM	798.7	3.8	799.2 ± 1.8	798.3 ± 1.6	0.73

[a]High RFI (n = 5), Low RFI (n = 6).

inevitable. Overall the IGER recorders worked quite well, greatly reducing labor requirements compared to visual observations. They provided the potential to acquire detailed and uninterrupted observation of grazing behavior for an extended period of time (~ 48hr).

Forbes et al. (1998) reported that cattle are most active in the early morning and late afternoon hours when temperatures are cooler. The greatest amount of inactivity occurs during the warmer periods of midday, as also observed in this study. In order to take full advantage of the most possible observations, behavioral data were collected from 6-h morning (0530-to-1130) and 6-h afternoon (1430-to-2030) activity periods.

An indirect measurement of daily forage intake in a grazing animal can be broken down to the mechanistic processes required for consumption (Erlinger et al., 1990). Therefore, variation in grazing behavior could be used as a tool to determine variation in forage intake on pasture. High and low RFI Brahman heifers in this study, previously evaluated for RFI in confinement, showed no difference in any of the grazing activities they were evaluated for. Grazing times in this study are similar to those reported by Forbes et al. (1998) in Brahman heifers (14-to-16 months of age) during the primary daytime grazing periods (0700-to-1100; 80-to-180 min and 1700-to-2000; 170-to-190 min). Efficient and inefficient heifers in the current study spent more time grazing in the afternoon than they did in the morning activity period ($P < 0.01$). Increased grazing activity in the afternoon activity period has also been reported in grazing studies by Erlinger et al. (1990) and Forbes et al. (1998) in both *Bos indicus* and *Bos taurus* breeds of cattle. Ruminating time was not significantly different between efficiency groups for either morning (*P* = 0.22) or afternoon (*P* = 0.57) activity periods, and all heifers spent equal time ruminating during these periods (*P* > 0.05). Ruminating time was proportionate to grazing time in the morning activity period, but heifers ruminated far less than they grazed in the afternoon. Idle time was not different between the efficiency groups in either morning (*P* = 0.49) or afternoon (*P* = 0.66) periods, but the overall mean idle times for all heifers were shorter during the afternoon activity period (*P* < 0.01). This is due to the increased amount of time spent grazing during this period. Idle time is defined as any activity that does not include grazing or ruminating activities. One limitation to the IGER grazing behavior recorders is that variation in time spent resting and traveling cannot be differentiated between, but could both be classified as idle time. This does not make idle time a true measure of inactivity. It is possible that animals of different efficiencies are behaving differently, or are more or less active than each other during this time. Variation in activity during these off periods may contribute to variation in maintenance requirements between efficient and inefficient animals. No differences were found in the rate at which heifers consumed forage, in bites/min, between efficiency groups for the morning (*P* = 0.48) or afternoon (*P* = 0.53) activity periods. All heifers grazed at a more vigorous rate in the afternoon than they did in the morning activity period (*P* = 0.04). Bite rates determined in this study are similar to those reported by Forbes and Coleman, (1993) (36-to-57 bites/min for cattle grazing Caucasian old world bluestem, and 37-to-56 for Plains old world bluestem), and Erlinger et al. (1990) (30-to-47 bites/min in 16-month-old *Bos taurus* breeds of heifers grazing summer Bermudagrass). Bite size is the only mechanism of forage intake that was not quantified in this study, making it a possible contributor to the variation in intake. Variation in the mass of forage consumed with each bite may contribute to variation in intake between animals that bite rate does not account for. The findings in this study reveal that variation in grazing behavior, measured during the major activity periods, does not help explain variation in RFI determined in confinement feeding.

Although there was no variation in grazing behavior between the efficiency groups during the primary activity periods, actual forage consumption is another potential source of variation in RFI. Herd et al. (1998) found no difference in intake on pasture between high and low RFI mature Angus cows. However, it was determined that the low RFI animals were more efficient because they had a 7 % heavier BW than the high RFI cows (618 ± 16.0 kg and 577 ± 11.0 kg; $P < 0.05$) with no difference in DMI ($P > 0.05$). Low RFI cows consumed an average of 12.5 ± 0.7kg/d and high RFI cows consumed an average of 13.2 ± 0.7 kg/d. Herd et al. (2005) in the backgrounding period on pasture, prior to feedlot entry, found that efficient line of steers, divergently selected based on post weaning RFI, were heavier at the end of the backgrounding period (418 vs. 409 kg; $P = 0.07$) and grew faster (0.66 vs. 0.64 kg/d; $P < 0.05$) than inefficient steers.

Brahman heifers did not differ in estimated intake as a portion of BW (kg DMI/100 kg of BW) for either alkane pair. This indicates that there is no difference in intake per unit of BW between efficient and inefficient animals grazing on pasture. There was no RFI*Day interaction for intake as a portion of BW when estimated by C31:32 alkane pairs ($P = 0.17$), but there was an RFI*Day interaction when intakes were determined by C33:32 alkane pairs (P = 0.02). The interaction occurs on d 7, indicating that forage intake was increasing for low RFI heifers from d 6-to-7, and intake was decreasing for high RFI heifers. Estimated intakes on d 7 were not significantly different (P = 0.80) between the efficiency groups. Intakes, as a portion of BW, were lower for the low RFI heifers on d 1 and d 3 (2.12 ± 0.09 vs. 2.48 ± 0.10 kg/100kg of BW; P = 0.02 and 2.23 ± 0.07 vs. 2.53 ± 0.07 kg/100kg of BW; P = 0.01) when determined by the C33:32 alkane pairs. Day did have a significant effect on estimated intake over the sampling period, which may be attributed to forage sampling error. Forage C33 alkane concentration decreased in samples collected on d 4 causing an increase in estimated forage intake on that day. Likewise, on d 5, C31 forage concentration increased, causing the estimated forage intake for d 5 to decrease. These differences were uniform over the treatment groups, so they did not have an effect on the individual treatments. These findings, although taken from a small sample set, suggest that selection for low RFI, determined in confinement, may not decrease DMI as a portion of BW in Brahman heifers on pasture.

There were no significant differences in apparent DMD between the RFI efficiency groups. Apparent DMD, determined by C31 alkanes were numerically less that apparent DMD determined by C33 alkanes. In confinement feeding, Brown (2005) reported that DMD had a negative correlation (r = -0.32; P < 0.05) with RFI, and that efficient animals tended (P < 0.13) to have a 6.6 % greater DMD than inefficient animals. Richardson et al. (1996) investigated the variation in DMD in British heifers and bulls during the RFI evaluation period. Although not significant, low RFI animals had a tendency to digest their feed better than the high RFI animals, resulting in a 2.3% decrease in daily feed requirements for an average calf in their study (450 kg steers). Richardson et al. (2004) following one generation of divergent selection for RFI in Angus cattle found a negative correlation (r = -0.44, $P < 0.05$) between DMD and RFI in these animals during an animal housing period while accessing metabolic processes.

Conclusion

The results of this study suggest that variation in grazing behavior, the variation in DMI as a portion of BW, and apparent DMD on pasture does not help explain variation in RFI determined in confinement feeding. Variation in grazing behavior between the efficiency groups are not explained in the main morning and afternoon activity periods, making the time spent grazing during the nighttime and midday periods possible sources of variation in RFI determined in confinement. Although DMI as a portion of BW was not significantly different (possibly due to a small n), numerical differences indicate that low RFI heifers may consume less forage as a portion of there BW than high RFI heifers. The findings in this experiment warrant the need for further investigation, with greater numbers, of the relationship between the variations in grazing behavior and forage intake on pasture between high and low RFI cattle. There does not appear to be an association between apparent DMD and efficiency based on RFI in Brahman heifers on pasture.

CHAPTER IV

CONCLUSIONS

The results of this study indicate that through selection based on RFI, producers can select for efficient animals without influencing rate of gain or BW measurements. These results also indicate that *Bos indicus* cattle appear to have efficiency traits similar to either *Bos taurus* or *Bos indicus* influenced breeds of cattle. Therefore utilization of RFI as a measure of feed efficiency should be as equally valid in *Bos indicus* cattle as it is in *Bos taurus* cattle. The major drawback to the use of other measures of efficiency is that selection for increased efficiency results in an increased rate of gain, as seen with FCR and PEG in this study. An increase in the rate of gain over a period of time potentially could increase mature BW. As seen in other studies, RFI was independent of ADG and all BW measurements. As a result of the feeding strategy and the lack of association between RFI and BW measurements, DMI was not significantly different between the efficiency groups. This shows that even when intake is limited, RFI is not associated with BW. However, low RFI heifers consumed less feed than predicted for their given level of production, compared to their inefficient counterparts. Although PEG and FCR have the potential to increase mature BW as a result of an increase in ADG, PEG shows to have a greater potential to decrease DMI than FCR, through selection. Temperament measurements taken at weaning were not related to any measures of feed efficiency in this study. Digestive kinetics, site of digestion, and apparent DMD did not appear to be different between the efficiency groups. There is sufficient enough evidence in the literature to warrant further investigation into the relationship between RFI and DMD. The results of this study suggest that variation in grazing behavior, the variation in DMI as a portion of BW, and apparent DMD on pasture does not help explain variation in RFI determined in confinement feeding. Variation in grazing behavior between the efficiency groups are not explained in the main morning and afternoon activity periods, making the time spent grazing during the nighttime and midday periods possible sources of variation in RFI determined in confinement. Although DMI as a portion of BW was not significantly different (possibly due to a small n), numerical differences indicate that low RFI heifers may consume less forage as a portion of there BW than high RFI heifers. The findings in this experiment warrant the need for further investigation, with greater numbers, of the relationship between the variations in grazing behavior and forage intake on pasture between high and low RFI cattle. There does not appear to be an association between apparent DMD and efficiency based on RFI in Brahman heifers on pasture.

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APPENDIX A

Table A.1. Fecal ADIA concentration, apparent DMD, and individual animal apparent DMD CV for heifers evaluated for RFI in Exp. I and II

Animal ID	Date Collected	Fecal ADIA, %	Apparent DMD, %	Apparent DMD SD	Mean Apparent DMD, %	Apparent DMD CV
4004	10/3/2005	1.98	57.46	11.05	56.20	19.66
4004	10/10/2005	2.42	54.13			
4004	10/17/2005	2.90	60.60			
4004	10/24/2005	2.70	66.31			
4004	10/31/2005	2.43	64.02			
4004	11/7/2005	2.08	45.51			
4004	11/14/2005	2.25	59.91			
4004	11/21/2005	2.60	65.60			
4004	11/28/2005	1.59	32.30			
4006	10/3/2005	2.16	61.11	12.44	54.78	22.72
4006	10/10/2005	2.86	61.22			
4006	10/17/2005	2.37	51.62			
4006	10/24/2005	2.12	57.10			
4006	10/31/2005	2.06	57.61			
4006	11/7/2005	2.07	45.41			
4006	11/14/2005	1.29	29.93			
4006	11/21/2005	3.17	75.44			
4006	11/28/2005	2.32	53.55			
4016	10/3/2005	3.69	77.21	13.66	49.19	27.77
4016	10/10/2005	2.12	47.76			
4016	10/17/2005	1.84	37.89			
4016	10/24/2005	1.89	52.04			
4016	10/31/2005	1.99	56.18			
4016	11/7/2005	1.83	38.06			
4016	11/14/2005	1.55	41.91			
4016	11/21/2005	2.16	58.46			
4016	11/28/2005	1.62	33.16			
4021	10/3/2005	2.13	60.46	20.07	51.97	38.62
4021	10/10/2005	1.64	32.34			
4021	10/17/2005	1.62	29.46			
4021	10/24/2005	3.97	77.13			
4021	10/31/2005	2.11	58.68			
4021	11/14/2005	2.10	57.03			
4021	11/21/2005	3.22	74.27			
4021	11/28/2005	1.47	26.37			
4026	10/3/2005	2.69	68.71	13.34	58.20	22.91
4026	10/10/2005	5.95	81.33			

Table A.1. Continued

4026	10/17/2005	2.33	50.83			
4026	10/24/2005	2.14	57.59			
4026	10/31/2005	2.38	63.38			
4026	11/7/2005	1.75	35.44			
4026	11/14/2005	2.13	57.61			
4026	11/21/2005	1.55	45.83			
4026	11/28/2005	2.88	63.11			
4029	10/3/2005	2.00	57.88	16.21	47.85	33.88
4029	10/10/2005	2.16	48.61			
4029	10/17/2005	2.14	46.43			
4029	10/24/2005	2.13	57.32			
4029	10/31/2005	1.98	55.86			
4029	11/7/2005	2.11	46.33			
4029	11/14/2005	2.68	66.29			
4029	11/21/2005	2.17	58.64			
4029	11/28/2005	1.20	10.18			
4036	10/3/2005	1.43	41.00	10.64	51.66	20.59
4036	10/10/2005	2.36	53.03			
4036	10/17/2005	1.93	40.80			
4036	10/24/2005	2.20	58.72			
4036	11/7/2005	2.24	49.56			
4036	11/14/2005	3.03	70.20			
4036	11/21/2005	1.42	41.18			
4036	11/28/2005	2.62	58.78			
4040	10/3/2005	1.49	43.64	9.73	49.90	19.49
4040	10/10/2005	2.06	46.03			
4040	10/17/2005	2.06	44.34			
4040	10/24/2005	2.45	62.90			
4040	10/31/2005	2.30	62.00			
4040	11/7/2005	1.98	42.82			
4040	11/14/2005	2.46	63.38			
4040	11/21/2005	1.53	41.63			
4040	11/28/2005	1.87	42.39			
4046	10/3/2005	1.83	54.15	8.91	52.37	17.02
4046	10/10/2005	2.07	46.48			
4046	10/17/2005	2.13	46.21			
4046	10/24/2005	2.72	66.57			
4046	10/31/2005	2.24	61.10			
4046	11/7/2005	2.40	52.81			
4046	11/14/2005	1.85	51.36			
4046	11/21/2005	1.97	56.51			
4046	11/28/2005	1.52	36.14			
4047	10/3/2005	1.89	55.48	14.03	42.48	33.03
4047	10/10/2005	1.23	9.99			

Table A.1. Continued

4047	10/17/2005	1.91	39.98			
4047	10/24/2005	1.99	54.41			
4047	10/31/2005	1.55	43.82			
4047	11/7/2005	2.08	45.65			
4047	11/14/2005	1.61	44.11			
4047	11/21/2005	1.94	53.95			
4047	11/28/2005	1.66	34.96			
4050	10/3/2005	1.83	54.08	11.35	49.13	23.09
4050	10/10/2005	1.59	30.22			
4050	10/17/2005	2.62	56.23			
4050	10/24/2005	1.87	51.33			
4050	10/31/2005	1.46	40.03			
4050	11/7/2005	2.08	45.69			
4050	11/14/2005	1.48	38.94			
4050	11/21/2005	2.35	65.83			
4050	11/28/2005	2.69	59.85			
4053	10/3/2005	1.58	46.64	9.84	50.93	19.31
4053	10/10/2005	1.69	34.21			
4053	10/24/2005	2.20	58.75			
4053	10/31/2005	2.33	62.47			
4053	11/7/2005	2.55	55.64			
4053	11/14/2005	2.00	54.90			
4053	11/28/2005	1.92	43.85			
4054	10/3/2005	2.44	65.58	9.20	58.26	15.79
4054	10/10/2005	2.99	62.82			
4054	10/17/2005	2.29	49.98			
4054	10/24/2005	2.26	59.79			
4054	10/31/2005	2.59	66.31			
4054	11/7/2005	2.66	57.48			
4054	11/14/2005	2.64	65.86			
4054	11/21/2005	2.16	58.51			
4054	11/28/2005	1.74	38.04			
4055	10/3/2005	1.56	46.19	9.94	49.65	20.02
4055	10/10/2005	2.26	50.86			
4055	10/17/2005	2.40	52.40			
4055	10/24/2005	1.93	53.06			
4055	10/31/2005	2.28	61.64			
4055	11/7/2005	2.24	49.57			
4055	11/14/2005	1.44	37.25			
4055	11/21/2005	2.01	63.01			
4055	11/28/2005	1.61	32.88			
4056	10/3/2005	1.95	56.77	12.16	48.22	25.22
4056	10/10/2005	2.27	51.14			
4056	10/24/2005	2.02	55.09			

Table A.1. Continued

4056	10/31/2005	2.19	60.06			
4056	11/7/2005	1.49	23.85			
4056	11/14/2005	1.42	36.65			
4056	11/21/2005	1.72	47.82			
4056	11/28/2005	2.11	54.37			
4057	10/3/2005	1.59	46.98	10.00	45.55	21.95
4057	10/10/2005	2.01	44.68			
4057	10/17/2005	1.74	34.38			
4057	10/24/2005	1.68	46.03			
4057	10/31/2005	2.05	57.49			
4057	11/7/2005	1.59	29.01			
4057	11/14/2005	2.13	57.75			
4057	11/21/2005	1.72	48.06			
4059	10/3/2005	1.05	19.61	13.63	52.70	25.87
4059	10/10/2005	2.77	59.86			
4059	10/17/2005	2.28	49.76			
4059	10/24/2005	2.22	59.16			
4059	10/31/2005	1.73	49.63			
4059	11/7/2005	3.55	68.13			
4059	11/14/2005	2.18	58.55			
4059	11/21/2005	1.99	54.99			
4059	11/28/2005	2.38	54.64			
4061	10/3/2005	1.38	38.87	14.09	47.30	29.79
4061	10/10/2005	1.93	42.53			
4061	10/17/2005	1.59	28.24			
4061	10/24/2005	2.78	67.28			
4061	10/31/2005	2.61	66.50			
4061	11/7/2005	1.79	36.82			
4061	11/14/2005	1.96	54.00			
4061	11/28/2005	1.93	44.14			
4063	10/3/2005	1.76	52.35	13.29	53.74	24.73
4063	10/10/2005	2.14	48.10			
4063	10/17/2005	2.30	50.31			
4063	10/24/2005	2.62	65.39			
4063	10/31/2005	3.20	72.69			
4063	11/7/2005	2.43	53.45			
4063	11/14/2005	2.79	67.68			
4063	11/21/2005	1.27	29.54			
4063	11/28/2005	1.93	44.13			
4066	10/3/2005	1.24	32.19	11.00	43.97	25.01
4066	10/10/2005	1.71	35.05			
4066	10/17/2005	1.94	41.13			
4066	10/24/2005	2.14	57.57			
4066	10/31/2005	2.17	59.79			

Table A.1. Continued

4066	11/7/2005	1.65	31.27			
4066	11/14/2005	1.73	47.79			
4066	11/28/2005	2.04	47.00			
4069	10/3/2005	1.72	51.03	10.38	48.11	21.57
4069	10/10/2005	2.33	52.37			
4069	10/17/2005	1.87	38.68			
4069	10/24/2005	1.78	49.03			
4069	10/31/2005	1.97	55.63			
4069	11/7/2005	2.55	55.72			
4069	11/14/2005	2.08	56.64			
4069	11/21/2005	1.77	49.33			
4069	11/28/2005	1.43	24.52			
4073	10/3/2005	1.78	52.85	12.45	44.46	28.01
4073	10/10/2005	1.86	40.26			
4073	10/17/2005	2.34	51.08			
4073	10/24/2005	1.70	46.73			
4073	11/7/2005	1.44	21.30			
4073	11/14/2005	1.98	54.55			
4076	10/3/2005	1.85	54.64	5.52	47.93	11.51
4076	10/10/2005	2.00	44.47			
4076	10/17/2005	2.18	47.60			
4076	10/24/2005	1.68	46.10			
4076	10/31/2005	2.15	59.30			
4076	11/7/2005	1.96	42.38			
4076	11/14/2005	1.72	47.62			
4076	11/21/2005	1.55	44.03			
4076	11/28/2005	1.79	45.19			
4077	10/3/2005	1.70	50.61	11.21	48.64	23.05
4077	10/10/2005	2.69	58.68			
4077	10/17/2005	2.08	44.84			
4077	10/24/2005	1.80	49.47			
4077	10/31/2005	1.86	52.98			
4077	11/7/2005	2.23	49.24			
4077	11/14/2005	1.27	28.93			
4077	11/21/2005	2.43	66.69			
4077	11/28/2005	1.69	36.29			
4079	10/10/2005	1.88	40.88	18.82	46.22	40.72
4079	10/17/2005	2.83	59.59			
4079	10/24/2005	2.33	60.99			
4079	10/31/2005	1.61	45.92			
4079	11/7/2005	1.86	39.27			
4079	11/14/2005	2.19	58.76			
4079	11/21/2005	2.19	59.11			
4079	11/28/2005	1.14	5.21			

Table A.1. Continued

5004	4/3/2006	2.32	61.96	9.31	54.54	17.07
5004	4/10/2006	2.56	66.31			
5004	4/17/2006	2.08	49.17			
5004	4/24/2006	2.95	59.61			
5004	5/1/2006	1.97	42.15			
5004	5/8/2006	2.38	64.33			
5004	5/15/2006	2.15	56.01			
5004	5/22/2006	2.32	59.13			
5004	5/29/2006	1.69	41.28			
5004	6/5/2006	1.67	45.42			
5005	4/3/2006	1.86	52.65	7.51	56.18	13.37
5005	4/10/2006	2.51	65.67			
5005	4/17/2006	2.07	48.97			
5005	4/24/2006	2.27	47.52			
5005	5/1/2006	2.49	54.34			
5005	5/8/2006	2.28	62.77			
5005	5/15/2006	1.76	46.26			
5005	5/22/2006	2.11	55.09			
5005	5/29/2006	2.73	63.77			
5005	6/5/2006	2.58	64.78			
5007	4/3/2006	1.93	54.27	9.40	54.33	17.30
5007	4/10/2006	2.09	58.86			
5007	4/17/2006	1.98	46.50			
5007	4/24/2006	3.11	61.69			
5007	5/1/2006	2.03	43.89			
5007	5/8/2006	2.01	57.89			
5007	5/15/2006	1.76	46.15			
5007	5/22/2006	1.62	41.39			
5007	5/29/2006	3.20	69.07			
5007	6/5/2006	2.50	63.59			
5010	4/3/2006	2.39	63.18	6.08	54.95	11.07
5010	4/10/2006	1.93	55.36			
5010	4/17/2006	2.06	48.63			
5010	5/1/2006	2.25	49.52			
5010	5/8/2006	1.72	50.69			
5010	5/15/2006	2.36	59.80			
5010	5/22/2006	1.89	50.01			
5010	6/5/2006	2.42	62.41			
5015	4/3/2006	1.52	42.02	11.74	56.54	20.77
5015	4/10/2006	1.79	51.78			
5015	4/17/2006	2.34	54.68			
5015	4/24/2006	2.02	41.00			
5015	5/1/2006	2.28	50.24			
5015	5/8/2006	1.97	56.98			

Table A.1. Continued

5015	5/15/2006	4.80	80.28			
5015	5/22/2006	2.55	62.84			
5015	5/29/2006	3.03	67.34			
5015	6/5/2006	2.18	58.29			
5019	4/3/2006	1.74	49.39	12.74	59.22	21.52
5019	4/10/2006	2.79	69.17			
5019	4/17/2006	1.81	41.54			
5019	4/24/2006	2.32	48.74			
5019	5/1/2006	2.37	51.98			
5019	5/8/2006	2.92	70.96			
5019	5/15/2006	2.83	66.49			
5019	5/22/2006	2.17	56.43			
5019	5/29/2006	3.04	83.07			
5019	6/5/2006	1.99	54.40			
5021	4/3/2006	1.83	51.95	9.44	55.29	17.08
5021	4/10/2006	3.15	72.66			
5021	4/17/2006	2.80	62.17			
5021	4/24/2006	1.93	38.45			
5021	5/1/2006	2.24	49.32			
5021	5/8/2006	2.29	63.05			
5021	5/15/2006	2.21	57.14			
5021	5/22/2006	1.84	48.56			
5021	5/29/2006	2.32	57.40			
5021	6/5/2006	1.90	52.17			
5026	4/3/2006	1.80	51.03	10.74	59.36	18.09
5026	4/10/2006	2.84	69.69			
5026	4/17/2006	2.46	56.95			
5026	4/24/2006	1.84	35.41			
5026	5/1/2006	3.60	68.40			
5026	5/8/2006	2.34	63.79			
5026	5/15/2006	3.34	71.64			
5026	5/22/2006	2.15	56.00			
5026	5/29/2006	2.33	57.49			
5026	6/5/2006	2.47	63.23			
5029	4/3/2006	2.20	59.96	3.97	63.76	6.23
5029	4/10/2006	2.30	62.51			
5029	4/17/2006	2.89	63.34			
5029	4/24/2006	3.05	60.96			
5029	5/1/2006	2.72	58.18			
5029	5/8/2006	2.74	69.08			
5029	5/15/2006	2.52	62.47			
5029	5/22/2006	2.76	65.64			
5029	5/29/2006	3.42	71.04			
5029	6/5/2006	2.56	64.45			

Table A.1. Continued

5036	4/3/2006	3.60	75.51	9.72	61.95	15.69
5036	4/10/2006	2.02	57.32			
5036	4/17/2006	2.84	62.70			
5036	4/24/2006	2.30	48.30			
5036	5/1/2006	2.28	50.18			
5036	5/8/2006	3.41	75.12			
5036	5/15/2006	2.62	63.88			
5036	5/22/2006	2.86	66.89			
5036	5/29/2006	2.08	52.41			
5036	6/5/2006	2.77	67.18			
5038	4/3/2006	1.72	48.68	12.36	56.35	21.93
5038	4/10/2006	2.56	66.41			
5038	4/17/2006	2.26	53.10			
5038	4/24/2006	2.78	57.23			
5038	5/1/2006	2.50	54.55			
5038	5/8/2006	1.56	45.66			
5038	5/15/2006	7.29	87.01			
5038	5/22/2006	1.76	46.31			
5038	5/29/2006	1.97	49.83			
5038	6/5/2006	2.01	54.74			
5039	4/3/2006	2.18	59.61	5.79	59.05	9.80
5039	4/10/2006	2.24	61.63			
5039	4/17/2006	2.54	58.35			
5039	4/24/2006	2.61	54.41			
5039	5/1/2006	2.48	54.24			
5039	5/8/2006	2.45	65.41			
5039	5/15/2006	3.23	70.66			
5039	5/22/2006	1.92	50.67			
5039	5/29/2006	2.31	57.10			
5039	6/5/2006	2.19	58.46			
5041	4/3/2006	3.12	71.78	10.03	57.37	17.49
5041	4/10/2006	2.02	57.47			
5041	4/17/2006	3.63	70.80			
5041	4/24/2006	1.97	39.48			
5041	5/1/2006	2.13	46.72			
5041	5/8/2006	1.79	52.54			
5041	5/15/2006	2.59	63.48			
5041	5/22/2006	2.10	54.88			
5041	5/29/2006	2.55	61.10			
5041	6/5/2006	2.04	55.42			
5042	4/3/2006	1.70	48.31	5.49	53.57	10.24
5042	4/10/2006	2.44	64.67			
5042	4/17/2006	2.19	51.68			
5042	4/24/2006	2.28	47.76			

Table A.1. Continued

5042	5/1/2006	2.58	55.90			
5042	5/8/2006	2.00	57.58			
5042	5/15/2006	2.20	56.98			
5042	5/22/2006	2.09	54.64			
5042	5/29/2006	2.03	51.14			
5042	6/5/2006	1.72	47.05			
5044	4/3/2006	3.34	73.65	13.66	54.47	25.08
5044	4/10/2006	2.66	67.63			
5044	4/24/2006	1.94	38.70			
5044	5/1/2006	1.70	33.13			
5044	5/8/2006	1.98	57.10			
5044	5/15/2006	2.18	56.63			
5044	5/22/2006	1.64	42.17			
5044	5/29/2006	2.67	62.85			
5044	6/5/2006	2.19	58.40			
5045	4/3/2006	3.70	76.19	13.92	60.60	22.97
5045	4/10/2006	2.49	65.40			
5045	4/17/2006	2.92	63.78			
5045	4/24/2006	1.68	29.14			
5045	5/1/2006	2.49	54.43			
5045	5/8/2006	2.96	71.42			
5045	5/15/2006	3.16	70.05			
5045	5/22/2006	3.22	70.62			
5045	5/29/2006	2.12	53.24			
5045	6/5/2006	1.88	51.70			
5047	4/3/2006	2.39	63.10	8.76	58.39	15.01
5047	4/10/2006	2.91	70.38			
5047	4/17/2006	2.89	63.32			
5047	4/24/2006	2.51	52.53			
5047	5/1/2006	3.39	66.45			
5047	5/8/2006	1.94	56.39			
5047	5/15/2006	2.50	62.17			
5047	5/22/2006	1.72	45.09			
5047	5/29/2006	1.77	44.16			
5047	6/5/2006	2.29	60.30			
5050	4/3/2006	3.37	73.85	10.56	60.97	17.32
5050	4/10/2006	2.99	71.20			
5050	4/17/2006	2.10	49.49			
5050	4/24/2006	2.24	46.84			
5050	5/1/2006	2.10	45.81			
5050	5/8/2006	2.57	67.02			
5050	5/15/2006	3.17	70.11			
5050	5/22/2006	2.92	67.55			
5050	5/29/2006	2.40	58.77			

Table A.1. Continued

5050	6/5/2006	2.22	59.10			
5051	4/3/2006	1.56	43.38	8.71	49.46	17.60
5051	4/10/2006	2.25	61.74			
5051	4/17/2006	2.03	47.89			
5051	4/24/2006	1.97	39.50			
5051	5/1/2006	2.21	48.64			
5051	5/8/2006	1.83	53.76			
5051	5/15/2006	2.59	63.47			
5051	5/22/2006	1.98	52.09			
5051	5/29/2006	1.56	36.54			
5051	6/5/2006	1.73	47.60			
5052	4/3/2006	2.17	59.45	9.60	54.14	17.72
5052	4/10/2006	1.85	53.39			
5052	4/17/2006	3.07	65.50			
5052	4/24/2006	2.06	42.08			
5052	5/1/2006	1.86	38.98			
5052	5/8/2006	1.77	52.22			
5052	5/15/2006	3.24	70.76			
5052	5/22/2006	1.91	50.45			
5052	5/29/2006	2.22	55.38			
5052	6/5/2006	1.94	53.23			
5053	4/3/2006	2.56	65.63	11.11	60.27	18.44
5053	4/10/2006	2.41	64.30			
5053	4/17/2006	2.44	56.68			
5053	4/24/2006	2.61	54.39			
5053	5/1/2006	1.79	36.53			
5053	5/8/2006	2.09	59.42			
5053	5/15/2006	3.30	71.34			
5053	5/22/2006	2.14	55.84			
5053	5/29/2006	2.52	60.63			
5053	6/5/2006	4.12	77.94			
5057	4/3/2006	3.04	71.04	18.32	54.21	33.80
5057	4/10/2006	2.49	65.40			
5057	4/17/2006	2.25	53.01			
5057	4/24/2006	2.41	50.64			
5057	5/1/2006	1.20	4.96			
5057	5/8/2006	2.22	61.76			
5057	5/15/2006	2.38	60.25			
5057	5/22/2006	2.33	59.40			
5057	5/29/2006	2.57	61.46			
5057	6/5/2006	1.98	54.16			
5059	4/3/2006	2.85	69.08	17.24	53.48	32.23
5059	4/10/2006	2.66	67.59			
5059	4/17/2006	2.03	47.75			

Table A.1. Continued

5059	4/24/2006	1.96	39.29			
5059	5/1/2006	1.38	17.60			
5059	5/8/2006	2.77	69.40			
5059	5/15/2006	3.37	71.91			
5059	5/22/2006	1.74	45.73			
5059	5/29/2006	1.90	47.88			
5059	6/5/2006	2.19	58.55			
5060	4/3/2006	2.33	62.24	15.92	55.56	28.66
5060	4/10/2006	2.33	63.02			
5060	4/17/2006	2.80	62.23			
5060	4/24/2006	2.28	47.72			
5060	5/1/2006	1.37	17.22			
5060	5/8/2006	3.08	72.52			
5060	5/15/2006	2.69	64.78			
5060	5/22/2006	2.66	64.40			
5060	5/29/2006	1.75	43.37			
5060	6/5/2006	2.17	58.08			
5065	4/3/2006	2.22	60.31	21.37	48.76	43.83
5065	4/10/2006	2.17	60.24			
5065	4/17/2006	2.37	55.40			
5065	4/24/2006	1.78	33.30			
5065	5/1/2006	1.07	-6.13			
5065	5/8/2006	2.01	57.94			
5065	5/15/2006	2.57	63.08			
5065	5/22/2006	1.88	49.64			
5065	5/29/2006	1.94	48.99			
5065	6/5/2006	2.59	64.86			
5069	4/3/2006	2.44	63.88	12.67	54.23	23.36
5069	4/10/2006	2.52	65.86			
5069	4/17/2006	2.22	52.30			
5069	4/24/2006	2.19	45.74			
5069	5/1/2006	1.62	29.65			
5069	5/8/2006	2.12	59.95			
5069	5/15/2006	2.60	63.58			
5069	5/22/2006	3.10	69.43			
5069	5/29/2006	2.01	50.86			
5069	6/5/2006	1.54	41.08			
5071	4/3/2006	2.33	62.20	13.87	59.85	23.18
5071	4/10/2006	3.00	71.32			
5071	4/17/2006	3.52	69.88			
5071	4/24/2006	2.92	59.26			
5071	5/1/2006	1.54	25.95			
5071	5/8/2006	2.77	69.40			
5071	5/15/2006	2.34	59.53			

Table A.1. Continued

5071	5/22/2006	3.54	73.28			
5071	5/29/2006	2.12	53.23			
5071	6/5/2006	2.00	54.48			
5072	4/3/2006	2.36	62.65	11.11	57.37	19.36
5072	4/10/2006	2.70	68.06			
5072	4/17/2006	2.51	57.86			
5072	5/1/2006	1.68	32.14			
5072	5/8/2006	1.81	53.22			
5072	5/15/2006	3.00	68.41			
5072	5/22/2006	2.35	59.64			
5072	5/29/2006	2.04	51.54			
5072	6/5/2006	2.44	62.79			
5074	4/3/2006	2.64	66.68	8.04	65.07	12.35
5074	4/10/2006	3.18	72.93			
5074	4/17/2006	2.38	55.60			
5074	4/24/2006	3.06	61.04			
5074	5/1/2006	2.43	53.20			
5074	5/8/2006	3.49	75.69			
5074	5/15/2006	3.95	76.01			
5074	5/22/2006	2.33	59.40			
5074	5/29/2006	2.98	66.77			
5074	6/5/2006	2.48	63.41			
5075	4/3/2006	2.12	58.46	6.31	56.01	11.27
5075	4/17/2006	2.58	58.89			
5075	4/24/2006	2.19	45.52			
5075	5/1/2006	2.34	51.32			
5075	5/8/2006	1.87	54.63			
5075	5/15/2006	2.81	66.25			
5075	5/22/2006	1.94	51.26			
5075	5/29/2006	2.21	55.18			
5075	6/5/2006	2.43	62.54			
5080	4/3/2006	2.74	67.87	16.93	60.04	28.21
5080	4/10/2006	2.67	67.73			
5080	4/17/2006	2.31	54.22			
5080	4/24/2006	2.27	47.56			
5080	5/1/2006	1.53	25.79			
5080	5/8/2006	2.83	70.09			
5080	5/15/2006	5.77	83.59			
5080	5/22/2006	4.34	78.17			
5080	5/29/2006	2.03	51.19			
5080	6/5/2006	1.98	54.13			
5082	4/3/2006	1.90	53.55	5.97	55.51	10.76
5082	4/17/2006	2.02	47.56			
5082	4/24/2006	2.17	45.14			

Table A.1. Continued

5082	5/1/2006	2.79	59.25			
5082	5/8/2006	1.95	56.65			
5082	5/15/2006	2.60	63.59			
5082	5/22/2006	2.22	57.33			
5082	5/29/2006	2.24	55.84			
5082	6/5/2006	2.31	60.68			
5086	4/3/2006	3.01	70.70	10.73	49.30	21.76
5086	4/10/2006	2.20	60.93			
5086	4/17/2006	2.23	52.43			
5086	4/24/2006	2.04	41.67			
5086	5/1/2006	1.84	38.29			
5086	5/8/2006	1.42	40.25			
5086	5/15/2006	1.50	36.71			
5086	5/22/2006	1.99	52.52			
5086	5/29/2006	2.01	50.68			
5086	6/5/2006	1.78	48.83			
5087	4/3/2006	2.41	63.48	5.92	60.64	9.76
5087	4/10/2006	2.16	60.07			
5087	4/17/2006	2.42	56.29			
5087	4/24/2006	2.64	54.85			
5087	5/1/2006	2.35	51.70			
5087	5/8/2006	2.06	58.81			
5087	5/15/2006	2.66	64.39			
5087	5/22/2006	2.33	59.34			
5087	5/29/2006	2.85	65.20			
5087	6/5/2006	3.28	72.25			
5088	4/3/2006	2.96	70.25	13.02	63.70	20.43
5088	4/10/2006	3.33	74.12			
5088	4/17/2006	7.16	85.22			
5088	4/24/2006	3.89	69.42			
5088	5/1/2006	2.81	59.56			
5088	5/8/2006	1.73	51.06			
5088	5/15/2006	3.31	71.35			
5088	5/22/2006	1.57	39.59			
5088	5/29/2006	2.33	57.57			
5088	6/5/2006	2.21	58.89			
5090	4/3/2006	2.11	58.29	11.14	57.62	19.33
5090	4/10/2006	5.35	83.90			
5090	4/17/2006	2.48	57.32			
5090	4/24/2006	3.17	62.42			
5090	5/1/2006	1.97	42.29			
5090	5/8/2006	1.79	52.64			
5090	5/15/2006	2.19	56.73			
5090	5/22/2006	2.23	57.46			

Table A.1. Continued

5090	5/29/2006	1.83	45.85			
5090	6/5/2006	2.24	59.35			
5091	4/3/2006	2.58	65.85	10.09	58.79	17.16
5091	4/10/2006	3.76	77.12			
5091	4/17/2006	2.07	48.94			
5091	4/24/2006	2.31	48.43			
5091	5/1/2006	2.32	50.96			
5091	5/8/2006	2.70	68.67			
5091	5/15/2006	1.94	51.11			
5091	5/22/2006	2.18	56.58			
5091	5/29/2006	2.11	53.11			
5091	6/5/2006	2.77	67.17			
5096	4/3/2006	2.26	61.09	8.73	57.26	15.24
5096	4/10/2006	2.79	69.18			
5096	4/17/2006	2.55	58.48			
5096	4/24/2006	2.04	41.76			
5096	5/1/2006	2.34	51.37			
5096	5/8/2006	2.23	62.08			
5096	5/15/2006	2.02	53.20			
5096	5/22/2006	2.07	54.34			
5096	5/29/2006	2.02	51.02			
5096	6/5/2006	3.04	70.12			
5098	4/3/2006	2.14	58.76	9.08	56.73	16.01
5098	4/10/2006	3.03	71.62			
5098	4/17/2006	2.06	48.57			
5098	4/24/2006	2.08	42.77			
5098	5/1/2006	2.32	51.05			
5098	5/8/2006	2.37	64.24			
5098	5/15/2006	1.84	48.67			
5098	5/22/2006	2.44	61.23			
5098	5/29/2006	2.87	65.54			
5098	6/5/2006	2.01	54.83			
5099	4/3/2006	2.25	60.84	11.89	58.56	20.31
5099	4/10/2006	3.07	71.91			
5099	4/17/2006	2.58	58.94			
5099	4/24/2006	1.71	30.28			
5099	5/1/2006	2.20	48.34			
5099	5/8/2006	2.21	61.67			
5099	5/15/2006	2.54	62.76			
5099	5/22/2006	2.32	59.11			
5099	5/29/2006	3.40	70.91			
5099	6/5/2006	2.32	60.83			

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